

THE DENTITIONS AND RELATIONSHIPS OF
THE SOUTHERN AFRICAN TRIASSIC MAMMALS,
ERYTHROTHERIUM PARRINGTONI AND
MEGAZOSTRODON RUDNERAE

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CONTENTS

	<i>Page</i>
I. INTRODUCTION	400
II. DENTITION OF <i>Erythrotherium parringtoni</i>	405
III. DENTITION OF <i>Megazostrodon rudnerae</i>	410
IV. MOLAR OCCLUSION	415
V. RELATIONSHIPS OF <i>Erythrotherium parringtoni</i>	423
VI. RELATIONSHIPS OF <i>Megazostrodon rudnerae</i>	423
1. <i>Sinoconodon rigneyi</i>	423
2. <i>Eozostrodon parvus</i> (= <i>Morganucodon watsoni</i>) and <i>E. oehleri</i>	426
3. <i>Docodon</i>	427
4. <i>Kuehneotherium praecursoris</i>	428
5. Amphilestinae	430
6. Haramiyidae	430
VII. CONCLUSIONS	431
VIII. ACKNOWLEDGEMENTS	435
IX. REFERENCES	435

SYNOPSIS

The dentitions of two southern African Triassic mammals, *Erythrotherium parringtoni* and *Megazostrodon rudnerae*, are described. On the basis of dentition alone, these forms seem to be closely related to the European and Chinese Triassic mammals, *Eozostrodon* (= *Morganucodon*) *parvus* and *Eozostrodon oehleri*. All of these mentioned forms are included in the Family Morganucodontidae. *Sinoconodon rigneyi*, also from the Chinese Triassic, should perhaps also be included in this family, although it has been placed in a separate family, the Sinoconodontidae. There is no justification for placing *Megazostrodon rudnerae* in this latter family.

One of the results of the reorganization and relative increase in mass and complexity of jaw musculature, which took place in the more advanced cynodonts, was that control and mobility of the lower jaw was increased. It is suggested that in the earliest and as yet undiscovered mammals, or in those cynodonts directly ancestral to mammals, this increased control permitted the longitudinal axis of the lower jaw to subscribe a triangular orbit during mastication. As a result of the transverse component of this orbit, the postcanine teeth of early mammals and their immediate ancestors were brought into closer contact than in their ancestral stock. This closer contact improved ability to break down food. Once a triangular orbit for the lower jaw was established, the characteristic features of mammalian dentitions evolved rapidly as a means of further improving efficiency. These features include single replacement of only some of the postcanine teeth, differentiation of the postcanine series into premolars and molars, consistent relationships of upper and lower molars with development of accurately matched shearing surfaces, and accurate alignment of adjoining molars.

It is shown that both the earliest known therian mammal, *Kuehneotherium*, and the early members of the non-therian mammalian stock, the Morganucodontidae, could be derived from a hypothetical ancestral group which possessed this suite of features. In the separate lines leading to therian and non-therian mammals, the ways in which the upper and lower molars contacted one another and the ways in which adjoining molars were aligned developed in slightly different patterns. These differences had far-reaching effects on the course of subsequent evolution of molar patterns and occlusion in therian and non-therian mammals.

I. INTRODUCTION

FIVE genera of Triassic mammals have been described, *Eozostrodon* (= *Morganucodon*),¹ *Kuehneotherium*, *Erythrotherium*, *Megazostrodon* and *Sinoconodon*.² (Selected papers dealing with these five genera are Kühne (1958), Crompton & Jenkins (1968), Hopson & Crompton (1969), Kermack, Kermack & Mussett (1968), Parrington (1971, 1973), Mills (1971), Crompton (1964), Patterson & Olson (1961) and Kermack & Kielan-Jaworowska (1971)).

The purpose of this paper is to give a detailed account and interpretation of the dentitions of *Megazostrodon rudnerae* and *Erythrotherium parringtoni*. Preliminary accounts have already been published (Crompton 1964; Crompton & Jenkins 1968; Hopson & Crompton 1969). Recently the types of both genera have been further prepared and much additional information is now available. The specimens are important because they add to the meagre body of knowledge on Triassic mammals and because both types consist of nearly complete skulls and skeletons. With full preparation it will be possible to give a skeletal reconstruction of two early mammals. This reconstruction has not previously been possible because, although the remains of *Eozostrodon parvus* are abundant, they are fragmentary. The skulls and skeletons will be described in later papers.

Detailed descriptions of the dentition of *Eozostrodon parvus* have recently been published by Parrington (1971) and Mills (1971). In a later paper Parrington (1973) has discussed differences between his and Mills' description of *Eozostrodon*. Mills (1971) has also given a detailed account of the dentition of *Eozostrodon oehleri* (= *Morganucodon oehleri*) (Rigney 1963). One of the important conclusions of Parrington's study is that *Eozostrodon parvus* had a mammalian pattern of tooth replacement with several of the milk molars being replaced by permanent premolars while the molars were never replaced. However, this form retained the reptilian feature of losing the anterior postcanines (in some cases even some of the anterior molars) either concurrent with or after the complete eruption of the postcanine dentition. Such detailed studies have tended to confirm the now generally accepted view that the Morganucodontidae ([= Eozostrodonidae], see Hopson 1970) are related to the non-therian mammalian radiation (i.e. docodonts, triconodonts,

¹ Unfortunately, there is no general agreement as to whether *Eozostrodon* and *Morganucodon* are synonyms. The case in favour of synonymy has been presented by Parrington (1971, 1973), and the case against by Kermack, Kermack & Mussett (1968) and Mills (1971). Whether the remains of the mammals from Wales, generally referred to as *Morganucodon watsoni*, and the type of *Eozostrodon parvus* from Somerset are included in the same taxon is perhaps not important, but it is confusing having both terms in current use. Parrington's case (1971, 1973) seems to be sound and in this paper *Eozostrodon* will be used in preference to *Morganucodon*.

² If the Haramiyidae prove to be mammals, the genera of this family would have to be added to the above list.

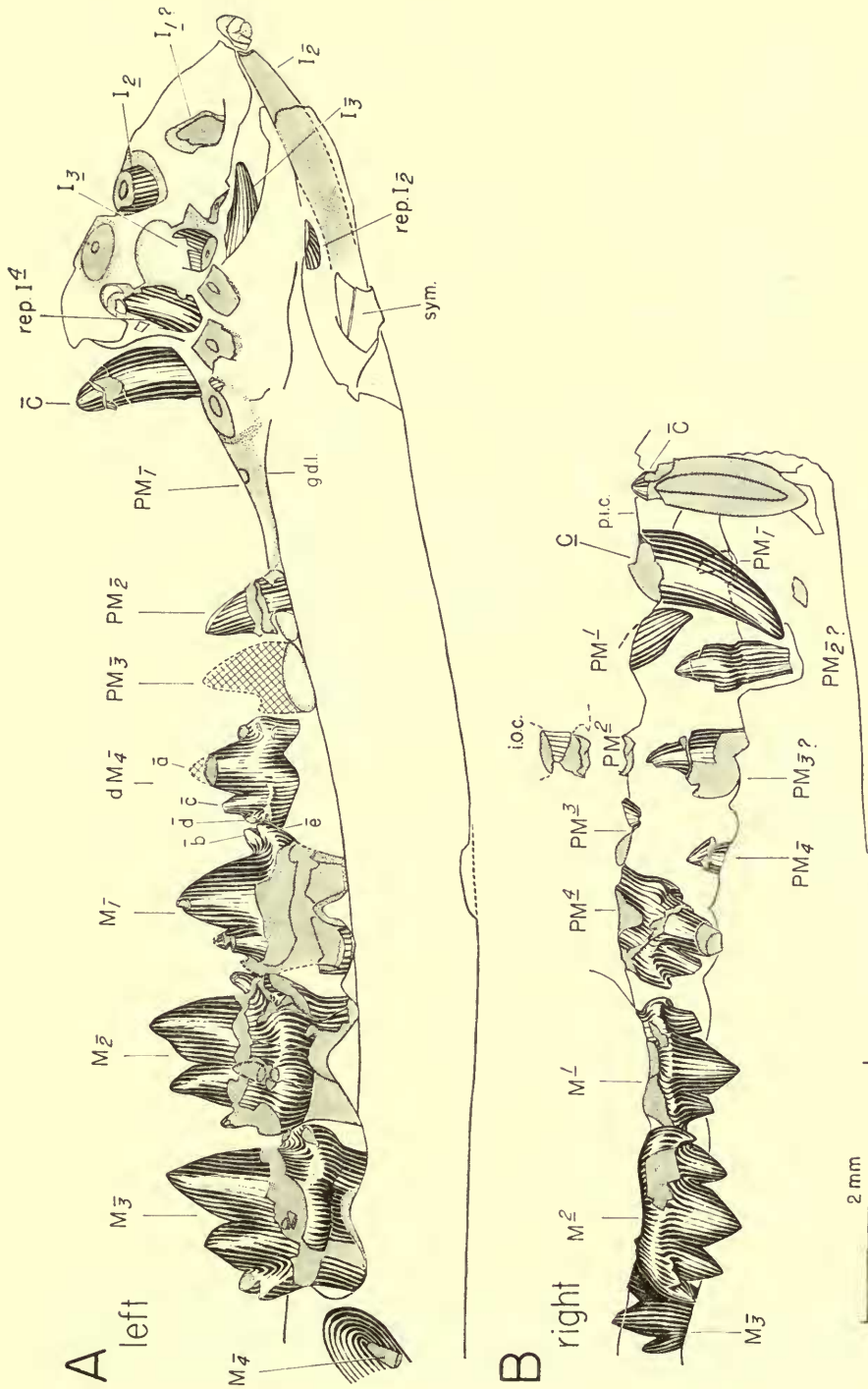
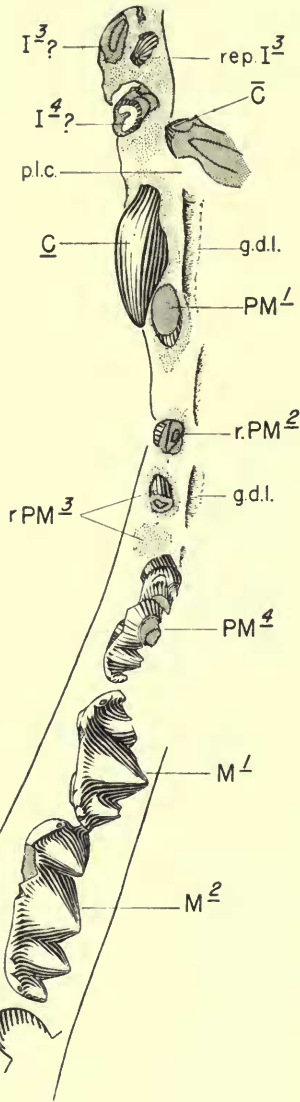


FIG. 1. *Erythrotherium parringtoni*. A. Internal view of the left dentary. B. External view of canine and postcanine dentitions on the right side. Abbreviations used in this and subsequent figures :

- | | | | | | |
|--------------------|--------------------------------|-----------------|------------------------------|--------------------|--------------------------------|
| a. PM ₁ | Alveolus of the first premolar | pa | Paracone | r. PM ₃ | Replacing third upper premolar |
| c.e. | Cutting edge | p.l.c. | Palatal pit for lower canine | rep. I | Replacing incisor |
| g.d.l. | Groove for dental lamina | pr | Protocone | sh.p. | Shearing plane |
| i.o.c. | Infraorbital canal | pr ^d | Protoconid | sty | Stylocone |
| med | Metaconid | p.u.p.c. | Pit for upper postcanine | sym | Symphysis |

A



B

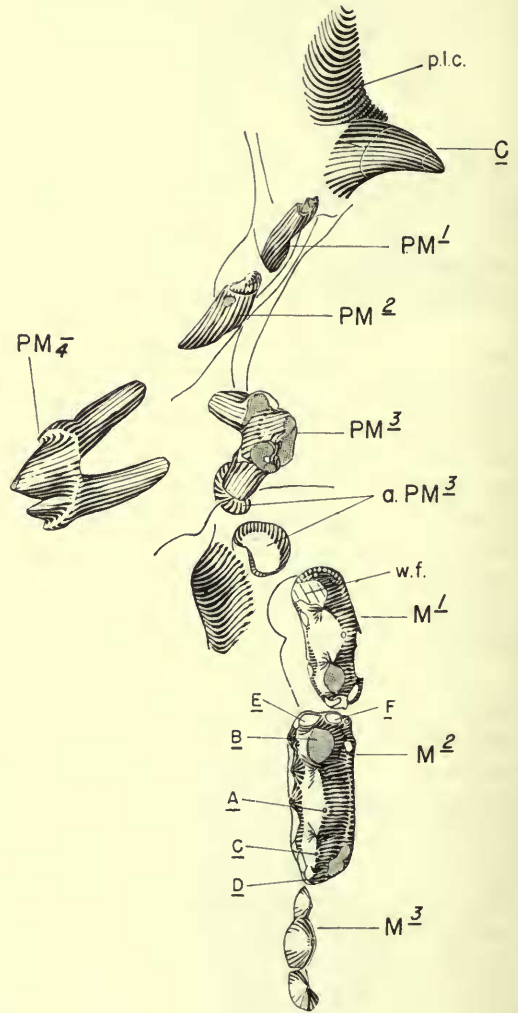


FIG. 2. *Erythrotherium parringtoni*. Crown views. A. Right upper dentition. B. Left upper dentition. (See Text-fig. 1 for abbreviations.)

multituberculates and monotremes) (Kermack 1967; Kermack & Kielan-Jaworowska 1971) whereas the Kuehneotheriidae are related to the therian mammalian radiation (including the Orders Pantotheria and Symmetrodonta (*sensu* Simpson 1945, 1971) as well as the Infraclasses Eutheria and Metatheria).

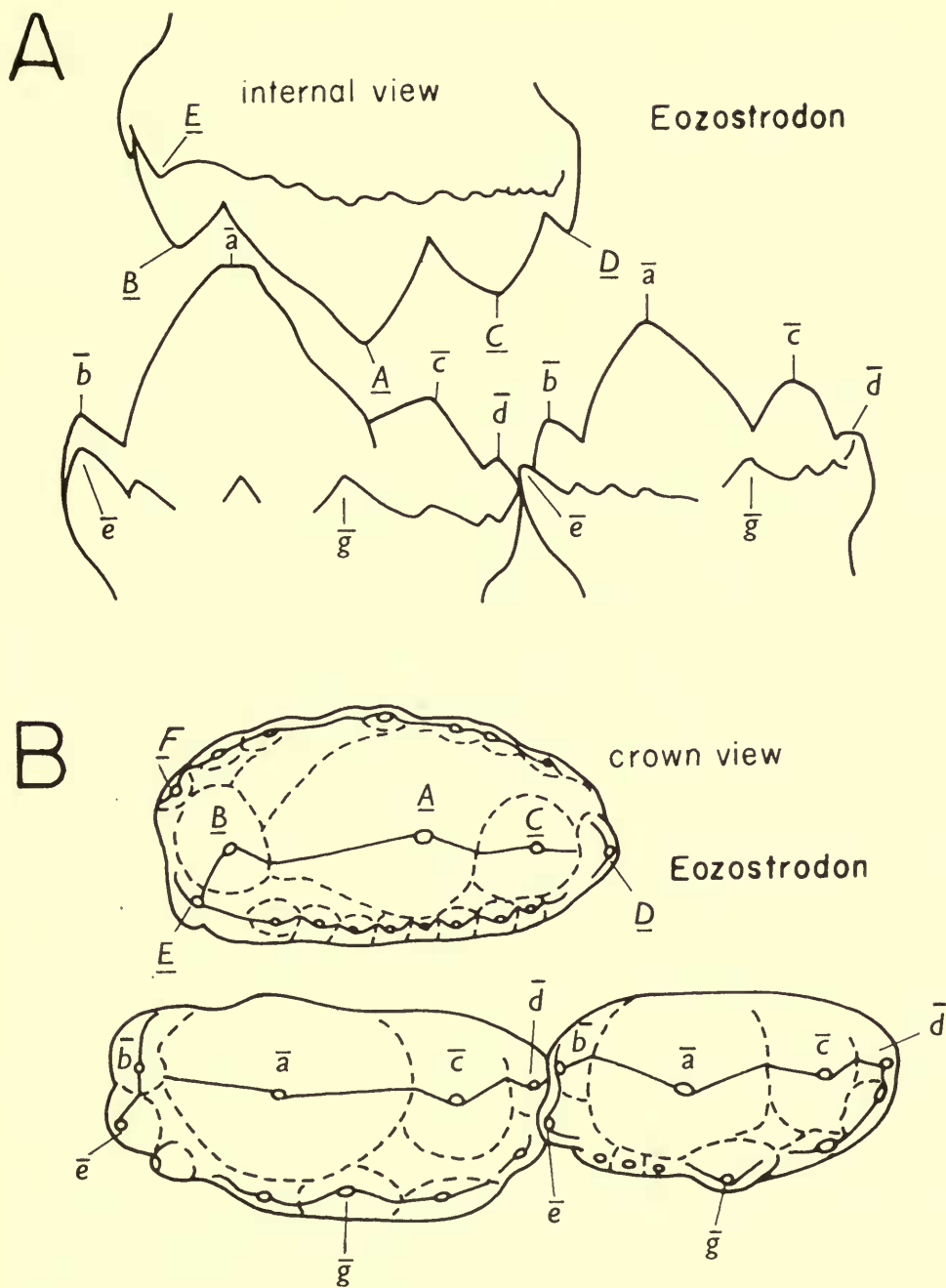


FIG. 3. *Eozostrodon parvus*. A. Internal, and B. Crown view of upper and lower molars to illustrate the positions of the cusps lettered \bar{a} to \bar{g} in the lower molars, and A to F in the upper molars. The same letters have been used in the description and illustration of the molars of *Erythrotherium parringtoni* and *Megazostrodon rudnerae*.

Conflicting views on the closeness of the relationship between the Kuehneotheriidae and Morganucodontidae (including *Eozostrodon*, *Sinoconodon*, *Erythrotherium* and *Megazostrodon*) have been published. The problem has recently been admirably reviewed by Clemens (1970). Parrington (1971, 1973), Crompton & Jenkins (1968), Hopson & Crompton (1969) and Hopson (1969) have suggested that a close relationship existed between these two families and that both could have been derived from a galesaurid (= thrinaxodontid) cynodont of early to middle Triassic age.³ *Probainognathus jenseni* (Romer 1969, 1970) from the middle Triassic of South America could well be, as has been suggested by Romer, a representative of the cynodont group from which mammals arose. *Probainognathus* is not highly specialized and the structure of the jaw articulation (Crompton 1972a), the structure of the postcanines, the tooth replacement pattern, the postcanine occlusion and the structure of the side wall of the braincase do not appear to debar it from being related to early mammals. Mills (1971), Kermack (1967) and Kermack & Kielan-Jaworowska (1971) are of the opinion that the differences between the two main groups of early mammals indicate that they are not closely related. If the ancestral stock from which the recognized orders of Triassic and Jurassic mammals arose did not lie close to the mammal-reptile boundary, it implies that many of the features which were not present in the ancestral group but which are common to both therian and non-therian mammals must have evolved independently in parallel in the two main phyletic lines. If, on the other hand, it is shown that a close relationship did exist between the Morganucodontidae and the Kuehneotheriidae, this implies that few of the mammalian osteological features (and, by implication, physiological features as well) evolved independently in parallel in the two lines.

The different phyletic lines of cynodonts are characterized by parallel acquisition of mammalian features and it is obvious that some of the common features of later non-therian and therian mammals (for example, the mammalian three-boned middle ear) must have evolved independently in these two groups (Hopson 1966). If it can be confirmed that the Kuehneotheriidae and the Morganucodontidae lay at the base of the two main mammalian radiations, and if they are shown to be closely related, it will mean that the line separating the therapsid and mammalian radiations can be more precisely drawn than was previously the case. It is well known that discrete characters previously thought to be diagnostic of mammals, such as the squamosodentary articulation, arose independently on more than one occasion (see Barghusen & Hopson 1970; Crompton 1972a) and this necessitates basing the diagnosis of what constitutes a mammal on a mosaic of several characters (Hopson & Crompton 1969; Hopson 1970).

The conflicting views of the origin of therian and non-therian mammals are at present based principally upon interpretation of the structure of the dentition and of the lateral wall of the braincase. In this paper the dentitions of the known Triassic mammals (excluding the Haramiyidae) will be discussed with reference to this problem and it is hoped in a later paper to review the structure of the braincase in therapsids and early mammals.

³ The haramiyids may prove to be related to both the eozostrodonids and the multituberculates (Hahn 1969).

II. DENTITION OF *ERYTHROTHERIUM PARRINGTONI*

(Text-figs. 1-3, Pl. 1)

A general description of the lower dentition of *Erythrotherium parringtoni* has already been given (Crompton 1964; Crompton & Jenkins 1968) so that it is not necessary to repeat that here.

This discussion will concentrate instead on additional details exposed by further preparation of the type specimen. The type is an immature animal in which some of the milk teeth were still functional.

Lower dentition

In the earlier description of the left mandible, a small pit was described behind the functional canine and it was suggested that this was the remnant of the root of an anterior postcanine tooth (Text-fig. 1A, PM₁). It now can be seen that the partially erupted tip of a tooth is present in the same position in the right mandible (Text-fig. 1B, PM₁). This appears to be a partially erupted first premolar. The pit in the left mandible lies in the groove for the dental lamina (Text-fig. 1A, g.d.l.) and it is concluded that the left first premolar would have erupted in this position later in life and that the preceding milk molar was shed shortly before death. The fifth and sixth postcanines (M₁ and M₂) on the left are fully erupted and are considerably larger than the fourth postcanine (dM₄). The fourth lower postcanine on the right (Text-fig. 1B) is only partially erupted and is identified as the fourth premolar (PM₄). The fifth, sixth and seventh lower postcanines (M₁ to M₃) are almost identical in structure to the molars of *Eozostrodon parvus*; it is concluded that they are the first, second and third molars. The fourth postcanine (dM₄) on the left is almost identical in crown structure to the molar teeth behind. This is in sharp contrast to the situation in *Eozostrodon* where the ultimate premolar is markedly different in size and form from the first molar. This suggests that it is a milk molar (see Parrington 1971, pl. 45, fig. D). The posterior accessory cusp,⁴ or cusp \bar{d} , of the fourth milk molar (Text-fig. 1A) fits into a shallow embayment between cusps \bar{b} and \bar{e} on the anterior surface of the first molar, forming a tongue-in-groove junction. The last milk molar and first molar lack Kühnecones (cusp \bar{g}). This area is extensively damaged on M₁ on the left side but is well preserved on the right (not figured). The Kühnecones of M₂ and M₃ are large. M₄ is only partially erupted and partially formed. The root of the second premolar on the right side is partially exposed; Mills (1971) has also found single-rooted second premolars in *Eozostrodon*. The crown of the third premolar was lost during recent preparation of the specimen and, unlike *Eozostrodon*, this tooth appears to be single-rooted, but it is not possible to establish beyond doubt that the second and third postcanines of *Erythrotherium* are premolars rather than molars.

⁴ In order to simplify the description of the postcanines, cusps will be referred to by the letters which were used in our previous discussion and description (Crompton & Jenkins, 1968; see Text-fig. 3 here). The cusps of upper teeth are indicated by capital letters with a line below (e.g. \bar{A}) and cusps of lower teeth by lower case letters with a line above (e.g. \bar{a}). Parrington has referred to the prominent cingulum cusp (\bar{g}) of the lower molars as the Kühnecone and this term will be used in this paper.

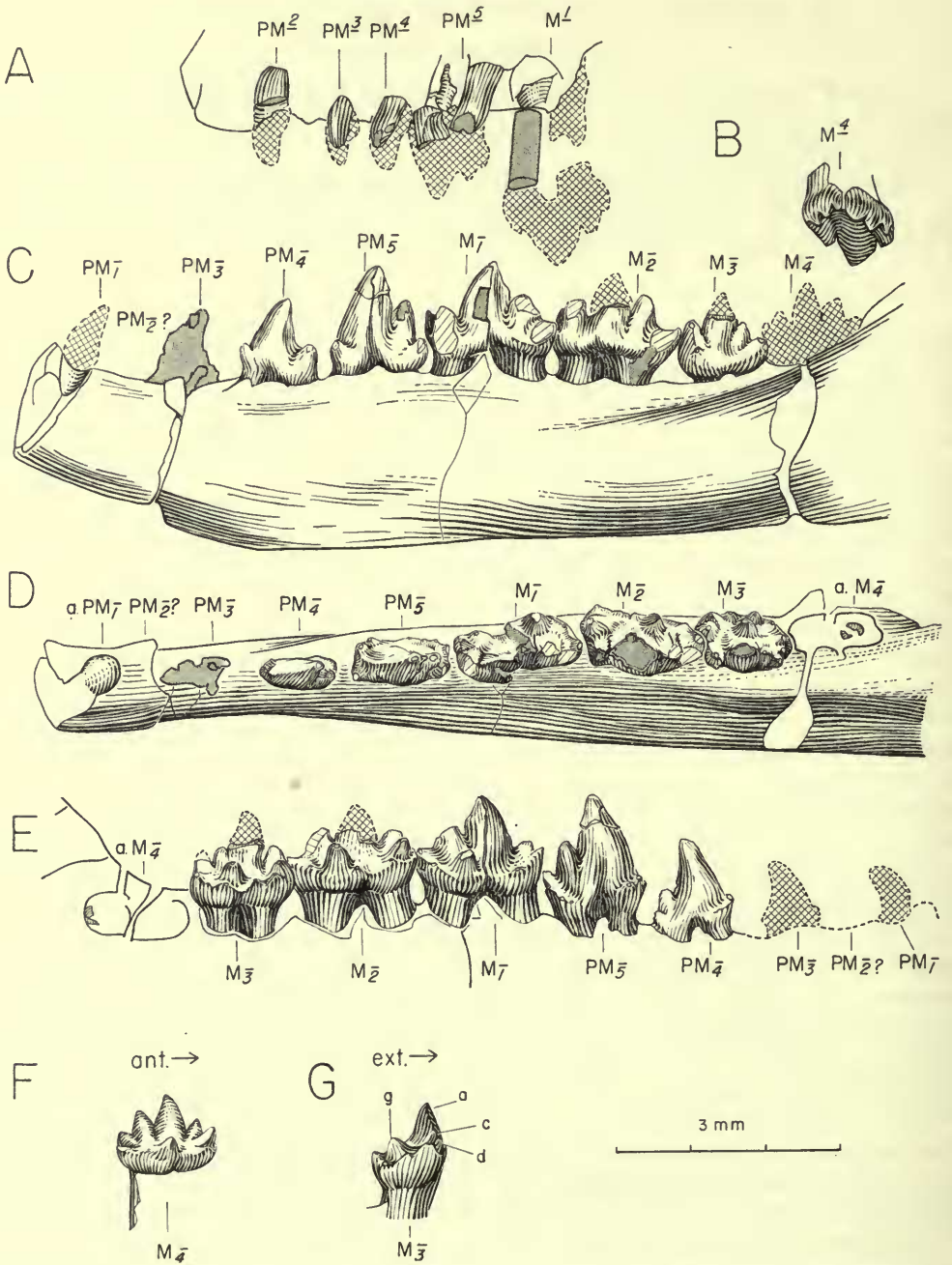


FIG. 4. *Megazostrodon rudnerae*. A. External view of the preserved portion of the upper left dentition. B. External view of isolated left M⁴. C. External view of left lower premolar-molar dentition. D. Crown view of the same. E. Internal view of the same. F. Isolated lower left M⁴. G. Posterior view of right lower M³.

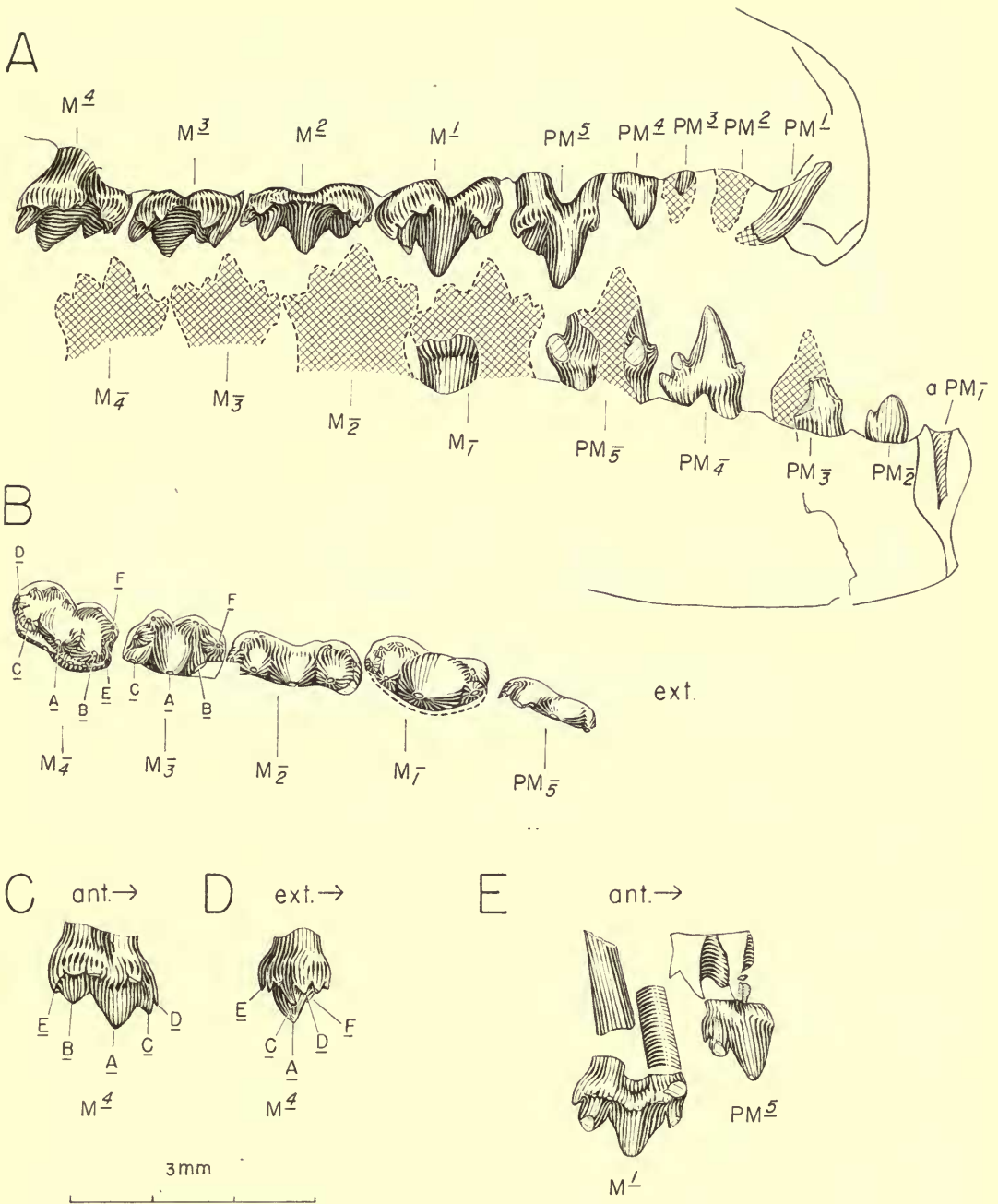


FIG. 5. *Megazostrodon rudnerae*. A. External view of right dentition. Outlines of the lower teeth based on a medial view. B. Crown view of last premolar and molars of right side. C. Medial view of right upper M^4 . D. Posterior view of the same. E. Internal view of left PM^5 and M^1 .

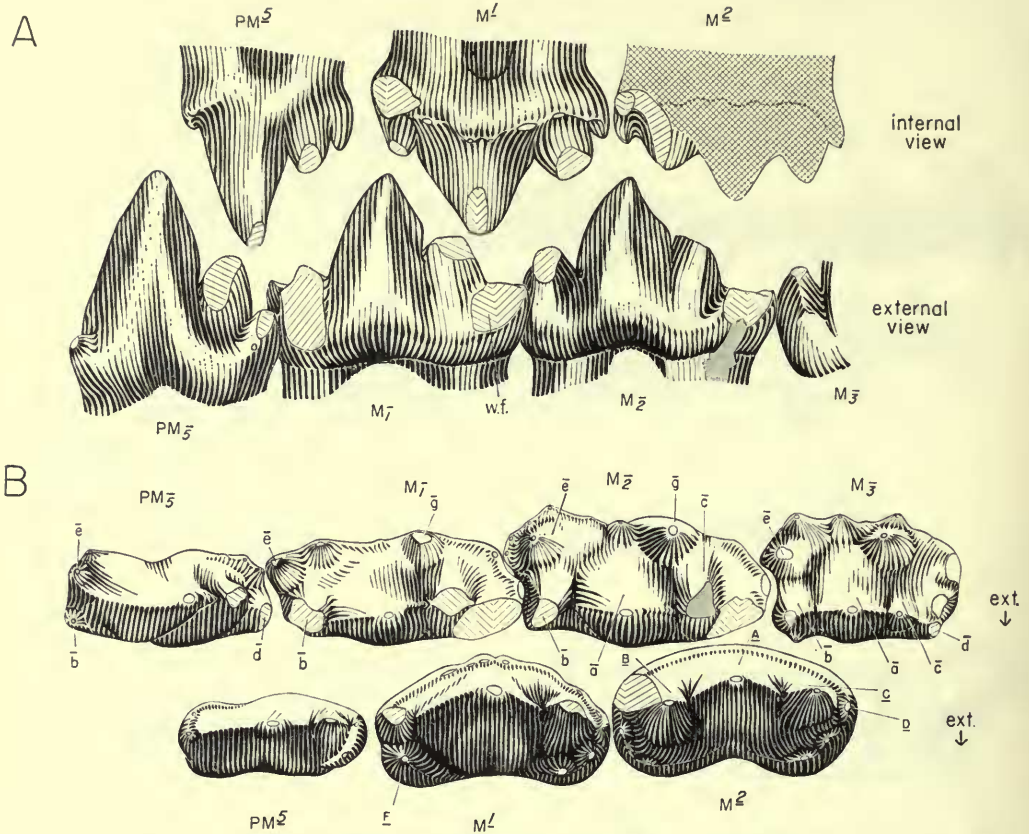


FIG. 6. *Megazostrodon rudnerae*. Reconstruction of postcanine occlusion. A. Internal view of upper $PM^{\bar{5}}$ - $M^{\bar{2}}$ and external view of corresponding lowers. B. Crown view of upper $PM^{\bar{5}}$ - $M^{\bar{2}}$ and lower $PM^{\bar{5}}$ - $M^{\bar{3}}$.

Upper dentition

The upper incisor region is not well preserved. On the left it is partially exposed by a fracture through the left premaxilla (Text-fig. 1A) and on the right only the last two damaged incisors are in position (Text-fig. 2A). There are at least four upper incisors. The ultimate incisor on the left and the penultimate incisor on the right have replacing incisors internally at their bases (rep. I). A partially erupted $PM^{\bar{1}}$ lies directly behind each of the functional upper canines (Text-figs. 1B, 2). The tips of these are directed forward and appear to touch the base of the functioning canine. This suggests that they may be replacing canines, but Parrington (1972, fig. 7) has shown that in *Eozostrodon* a replacing upper canine lies medial to the functional canine. For this reason, it is concluded that these erupting teeth are the first permanent premolars. A groove for the dental lamina lies in the maxilla medial to the functional canine and is confluent with the alveolus of the erupting first premolar (Text-fig. 2A, g.d.l.). Antero-medial to the upper functional canine, a

shallow pit (p.l.c.) is present in the palate (Text-figs. 2A, 2B). This accommodates the tip of the lower canine and is similar to the pit in the palate of *Eozostrodon parvus*, cynodonts, and several other therapsid groups. The second upper premolar is preserved only on the left (Text-fig. 2B); it is a single-rooted tooth with a small posterior heel on the crown. The third premolar is also only preserved on the left. It is a double-rooted tooth with a tricuspid crown and a small heel behind the posterior cusp. The fourth premolars are preserved on both sides (Text-figs. 1B, 2); the right one is *in situ* and that on the left is displaced but preserved in the matrix near its alveolus. The crown is dominated by a main cusp having its anterior border considerably longer than its posterior. A small anterior cusp is present and is closer to the base of the tooth than the small cusp which lies posterior to the main cusp. Cusp C is followed by a smaller cusp D. A faint cingulum is present on the antero-external and postero-external surfaces of the crown. The tips of the roots are not expanded, but this does not necessarily invalidate a close relationship between *Erythrotherium* and *Eozostrodon*. Parrington (1973) pointed out that the expansion of the tips of the molar and premolar roots in *Eozostrodon* is a feature developed in mature specimens.

The first molar is preserved *in situ* on both sides (Text-fig. 1B, 2). It is considerably larger than, and differs markedly from, the fourth premolar. The anterior border of the main cusp A is longer than the posterior, but the discrepancy is not as marked as in the fourth premolar. Cusp B is larger than that of the fourth premolar; a slightly cuspidate cingulum is confined to the anterior and posterior regions of the tooth and a faint cingulum is present along the entire internal surface. The tip of cusp B has been worn down (w.f.) forming an oblique facet facing downward and inward (Text-fig. 2B).

The second molar (Plate 1, Text-figs. 1B, 2) is the largest of the preserved teeth. Cusps B and C are, relative to cusp A, larger than in the first molar. The front of the tooth is broad and supports two small cusps (E and F) with a slight embayment between them. This, together with cusp D of the first molar, forms a junction between the two molars not unlike that described for the lowers. The external cingulum is poorly developed. The partially formed and partially erupted crown of the third molar is present on the left but this tooth is not preserved on the right. The spacing between the tips of the main cusps is less than in the second molar so that when fully formed this tooth would have been smaller than the second molar.

The dental formula for *Erythrotherium parringtoni* appears to be: $I_{\frac{4+?}{3+?}}^{\frac{4+?}{3+?}} C_1^1 PM_{\frac{4}{4}}^{\frac{4}{4}} M_{\frac{3+?}{4}}^{\frac{3+?}{4}}$. In the type specimen, the erupting first premolar lies directly behind the canine and there is therefore no evidence that five teeth (premolars or milk molars) were present in a less mature specimen.

On the basis of a study of the morphology of numerous molar teeth, Mills (1971) has correctly pointed out that *Erythrotherium parringtoni* and *Eozostrodon parvus* are almost identical and that the distinctions which I had previously listed (1964) are no longer valid reasons for placing the African form in a separate genus because all the features of *Erythrotherium* molars are encountered in a large sample of *Eozostrodon* molars. However, there are reasons for retaining the southern African form in a separate genus. In *Eozostrodon* (Parrington 1971, 1972; Mills 1971) the first

upper molar is the same size or even slightly smaller than the ultimate premolar. Mills (1971 : 34) has stated that the ultimate premolar '... is as long as the longest molar and rather higher'. In *Erythrotherium*, on the other hand, the ultimate upper premolar is smaller than the first molar; this may be a characteristic of the southern African eozostroodontids (see discussion of *Megazostrodon* below). In the lower jaw of *Erythrotherium*, the last premolar is only partially erupted and its crown structure is not known and so cannot be compared with *Eozostrodon*. In *Erythrotherium*, the Kühnecone is absent on the first lower molar whereas in *Eozostrodon parvus* it is present.

The number of partially formed, partially erupted and replacing teeth establishes beyond doubt that the type of *Erythrotherium* was a young animal. For this reason it is not possible to determine the occlusal pattern. However, wear on M¹ suggests that when the jaws were closed, the main cusp (\bar{a}) of the lower molar lay anterior to the cusp \underline{B} of an upper molar rather than behind it as is the case in *Eozostrodon*. A similar situation to that of *Erythrotherium* has been described for *Megazostrodon* and this is discussed further on p. 415.

III. THE DENTITION OF *MEGAZOSTRODON RUDNERAE*

(Text-figs. 4-6, Pls. 1, 2)

Preliminary descriptions of the dentition of *Megazostrodon rudnerae* have been given in previous papers (Crompton & Jenkins 1968; Hopson & Crompton 1969). Subsequently the skull of the type has been further prepared as extensively as possible without endangering the specimen.

Lower dentition

It is difficult to be certain about the number of lower premolars because the incisors and canine are not preserved. There appear to be four premolars on the left (Text-fig. 4), and five on the right (Text-fig. 5A). The first premolar is represented by the posterior rim of an empty alveolus (a. PM₁) on both sides. It is possible that this is the remnant of a canine alveolus rather than a premolar alveolus. If this proves to be the case, the premolar count would be four instead of five and the canine would have been a very small tooth. The second premolar on the right is small with a minute posterior heel. The corresponding tooth is absent on the left and a small diastema separates the alveoli for the first premolar and the third premolar (Text-figs. 4, PM₂?). There is no evidence in this diastema of a bony plug which would indicate the presence of a resorbed root. The third premolar is larger and has a slightly recurved main cusp and a small posterior heel. The fourth premolar is well preserved on both sides. A small cusp \bar{b} is present in front of and at the base of the main cusp. A small cingulum runs posteriorly from this cusp on the inner side of the tooth. A larger cusp \bar{c} lies at a higher level than cusp \bar{b} immediately behind the main cusp \bar{a} . At a lower level and postero-medial to cusp \bar{c} a minute cusplule \bar{d} is present. The outline of the fifth lower premolar is almost identical to that of the fourth premolar (Text-figs. 4, 6), but there are some interesting

differences. Two small cusps, \bar{b} and \bar{e} , lying at approximately the same height are present on the front of the tooth at the base of the main cusp. They are separated by a shallow embayment. A short cingulum supporting a small cusp runs backward from cusp \bar{e} on the internal surface of the tooth. A prominent cusp \bar{c} lies behind the main cusp. A smaller cusp \bar{d} lies behind and slightly on the external side. From this cusp, a cingulum supporting several cusps runs downward and forward on the internal surface of the crown. The most posterior cusp on this cingulum is at a slightly lower level than cusp \bar{d} and the ridge connecting these two cusps is slightly concave. The external surface of cusp \bar{e} of the first molars butts against this region of the fifth premolar. Wear is present on the external surface of the tips of cusps \bar{c} and \bar{d} (Text-fig. 6).

The first lower molar differs distinctly from the fifth premolar; it is larger and has a prominent internal cingulum supporting a large Kühnecone (Plate 1). Cusp \bar{a} is relatively less prominent than cusp \bar{a} in the fifth premolar. The outer surface and tip of cusp \bar{b} is fairly heavily worn (Text-fig. 6). Cusp \bar{e} is a prominent feature of the crown and is far larger than in any of the other known eozostroodontids; it projects further forward than cusp \bar{b} . Consequently, in external view, cusp \bar{b} does not appear to be a small cingular cusp as it does in *Eozostrodon parvus* (Text-fig. 3) where it is relatively small and where cusp \bar{e} is smaller than in *Megazostrodon*. A lingual cingulum runs backward for a short distance from cusp \bar{e} and supports a small cuspsule. The Kühnecone is extremely large and not connected by either ridges or cingula to the other cusps of the crown. The tip of cusp \bar{c} is slightly worn, as is the outer surface of the tooth behind cusp \bar{c} (Text-fig. 6, w.f.). A distinct cusp \bar{a} of the upper first molar (Text-fig. 6A) must have lain external to the gap between cusps \bar{c} and \bar{d} when the jaws were closed. A wider space separates the base of cusp \bar{c} from the posterior margin of the tooth than is found in the typical lower molars of *Eozostrodon parvus*. In the crown view (Text-fig. 6B) this region is also narrower than in *E. parvus* where the posterior region of the crown of the lower molars is usually wider than the remainder of the crown (Text-fig. 3B). This region in *Megazostrodon* is reminiscent of a 'talonid' heel of early therian mammals such as *Kuehneotherium* (Text-fig. 7B).

The second molar of *Megazostrodon* is well preserved on both sides although on the right only the medial view is exposed. The crown structure is very similar to that of the first molar but there are differences. Cusp \bar{e} is larger and more widely separated from cusp \bar{b} . The anterior border of cusp \bar{e} lies further forward of cusp \bar{b} than it does in the first molar. A wide embayment is present on the front surface of the crown between cusps \bar{e} and \bar{b} . This receives the 'talonid' of the first molar (Text-fig. 6B). A prominent cingulum is present on the antero-internal surface of cusp \bar{e} . This cingulum is cuspidate with the largest cuspsule postero-medial to cusp \bar{e} . Beyond this point it continues backward to the base of the Kühnecone where it is terminated by a cuspsule. The tip of cusp \bar{c} and the external surface of the tooth behind this cusp are worn and cusp \bar{d} has been obliterated. A wide 'talonid' shelf separates the base of cusp \bar{c} from the posterior margin of the tooth (Text-fig. 6A). On the left M_2 the crown surface of the 'talonid' shelf appears to be worn but this does not appear to be

the case for the corresponding tooth on the right (Plate 1). The posterior tip of the 'talonid' fits into a shallow embayment between cusps \bar{b} and \bar{e} of the third molar.

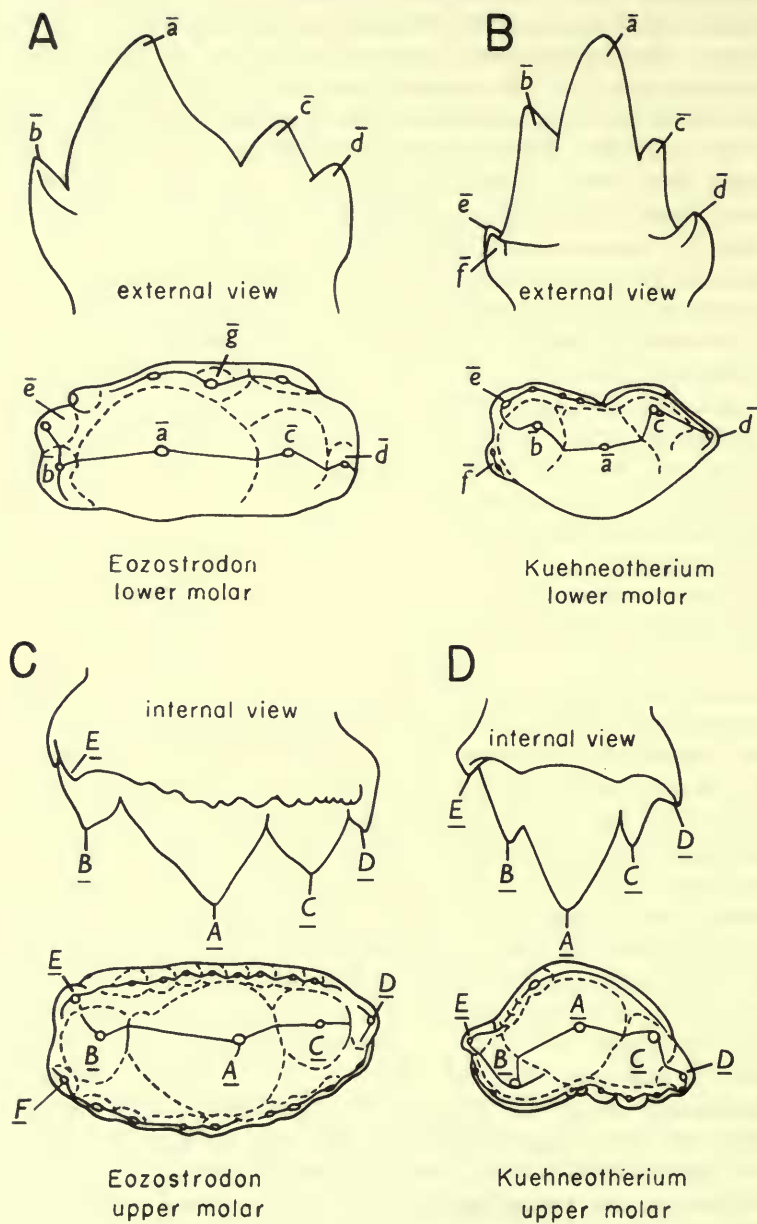
In crown view, the third molar is shorter and more bulbous than the second molar. Cusps \bar{b} and \bar{e} are large and a prominent cingular cusp is present internal to cusp \bar{e} , but this does not extend onto the anterior surface of cusp \bar{e} as is the case on the second molar. A striking feature of this tooth is the internal cingulum which extends without interruption from cusp \bar{e} to cusp \bar{d} and lies internal to the Kühnecone (Pl. 1). This cingulum supports six cuspules in addition to cusps \bar{d} and \bar{e} . A prominent cusp is present internal to the Kühnecone. Consequently the Kühnecone in this tooth would be defined not as an enlarged cingular cusp, as in the first and second molars of *Megazostrodon* or in the molars of *Eozostrodon parvus*, but as a crown cusp. In Text-fig. 4G the third lower molar as seen from behind is illustrated. This clearly shows the great width of the tooth medial to the main cusp (\bar{a}) and the cingular cusp outside the Kühnecone (\bar{g}). The cingula present antero-internal to cusp \bar{e} on the second molar and internal to the Kühnecone on the third molar illustrate how within one individual the same cusp can be defined either as a cingular or a crown cusp. Cusp \bar{c} of the third molar is minute and this clearly distinguishes this tooth from the other molars. Other than small wear facets on the tips of cusps \bar{b} and \bar{d} , this tooth shows no signs of wear. A small cusp is present on the external surface of cusp \bar{b} (Text-fig. 6). In both right and left rami a double-rooted empty alveolus lies behind the third molar. The bones of the left side of the snout and the posterior part of the skull were macerated slightly before fossilization. Lying among these bones is an isolated molar. It has been identified as the fourth left lower molar (Text-fig. 4F) because it differs from the morphology of all the known upper molars; it is the right size for the empty alveolus and it possesses a well-developed Kühnecone. Unfortunately, only the internal view and part of the external view of this tooth could be exposed. The tooth is similar to the first and second molars in having cusp \bar{c} larger than cusp \bar{b} . This contrasts with the condition in the third lower molars. The internal cingulum is poorly developed. The third molar is 'odd man out' in that cusp \bar{c} is reduced, a cuspule is present on the external surface, and the Kühnecone has the appearance of a crown cusp rather than a cingular cusp. The marked difference between the third molar and the adjoining molars is also a feature of the upper dentition of *Megazostrodon*.

Upper dentition

As in the lower jaw, it is difficult to be certain about the number of premolars because an upper canine is not preserved. The first postcanine tooth preserved on the right side has been identified as the first premolar (Text-fig. 5A). Its tip is worn and its single root is partially exposed. It is followed by a gap that appears to contain the remnants of the root of the second premolar. On the left side (Text-fig. 4A) the root of the corresponding tooth and part of its alveolus are preserved. This is also a single-rooted tooth. The third premolar on both sides is represented by a worn nubbin of dentine. The fourth premolar on the right side is well preserved whereas that on the left is damaged. It consists of a main cusp followed by a small posterior heel near the base of the tooth. This tooth appears to be single-rooted.

The external surface of the fifth premolar is preserved on the right side (Text-fig. 5A) and the internal surface preserved on the left (Text-fig. 5E). The crown is dominated by a main cusp. A minute capsule is present in front at the base of the crown and two cusps, both larger than the anterior one, are present behind the main cusp. Of these, the first is larger. A small external cingulum runs forward from the posterior cusp and terminates above the gap between cusps B and A. Unlike the first four premolars, this tooth is double-rooted. The external view of the first molar is also exposed on the right side (Text-fig. 5A), and the internal view on the left (Text-fig. 5E). The main cusp dominates the crown in this tooth and its anterior border is longer than the posterior, reflecting the discrepancy in size between cusps B and C. A small cusp is present on the external surface of cusp B. Cusp C is followed by a smaller cusp D. A short external cingulum runs forward from D and supports two small cusps. The anterior and posterior portions of the external cingulum do not meet and, consequently, in crown view the tooth is bean- or kidney-shaped (Text-fig. 6B). A narrow internal cingulum runs backwards from the base of cusp B to the tip of cusp D. It is slightly crenulated and best developed above the tip of cusp A (Pl. 2). Oblique wear facets are present on the internal surface of the tips of cusps B and C and on the internal cingulum above cusps C and B (Text-fig. 6A). Poorly developed wear facets are also present on the internal surface of cusp A near the tip of this cusp and on the internal surface of the tooth immediately above cusp B. The internal surface of the tooth is markedly convex in crown view and the three main cusps form an obtuse angle, rather than being in line. This is in contrast to the condition in M^4 . Both of the roots of the left first molar were exposed by a fracture (Text-fig. 5E). These taper towards their tips and lack the characteristic 'club feet' of *Eozostrodon*. As all the molars of the type of *Megazostrodon* are fully erupted, it was presumably a mature individual. Expansion of the root tips is found only in mature individuals of *Eozostrodon* and the absence of this feature in *Megazostrodon* is a clear difference between the two genera.

M^2 is characterized by the nearly equal development of the crown in front of and behind the main cusp so that B and C are nearly equal in height. A well-developed cingulum is present on the antero-external surface of the crown. This cingulum terminates above the gap between cusps A and B and supports three cusps. The internal surface of cusp B is worn and if a cusp E were present, it has been obliterated by wear (this cusp is present on M^4). A well-developed and bulbous external cingulum runs forward from cusp D and terminates before reaching the midpoint of the tooth. Consequently, in crown view the tooth has the same bean-shaped appearance as M^1 , except that it is slightly more pronounced. The internal surface of M^2 could not be fully exposed. As in the first molar, the principal cusps are not in line. M^3 is shorter and wider than M^2 or M^4 . The external cingulum is greatly enlarged and supports four distinct cusps, two anterior to the midpoint and two posterior to the midpoint. Of these, the anterior cusp F (Text-fig. 5B) is the largest and it is larger than cusp B. It is followed by a smaller cusp. The two postero-external cusps are sharply pointed and smaller than the anterior. Cusp D is absent and the external cingulum terminates at the base of cusp C. Immediately above the tip of the main cusp, the external cingulum is absent so that a V-shaped valley



← Anterior

FIG. 7. Comparison of the upper and lower molars of *Kuehneotherium* and *Eozostrodon*.

separates the anterior and posterior portions of the external cingulum. Because of the large size of the cingulum and cingular cusps, prominent antero-lateral and postero-lateral basins separate the base of the main cusps from the cingular cusps. The antero-internal edge of the crown in front of cusp B is heavily worn. The fourth upper molar is longer and narrower than M^3 . The external cingulum is well developed and supports four large cusps separated by a V-shaped valley at the midpoint of the tooth. A small cusp D is present. A marked feature of M^4 is that the tip of the main cusp lies behind the midpoint of the external surface (this is noticeable to a lesser extent in M^3 in Text-fig. 5A). M^4 is preserved on both sides (Text-figs. 4B, 5A); consequently this feature does not appear to be due to postmortem crushing. Part of the medial view of the right M^4 is exposed (Text-fig. 5C). A well-preserved cusp E is present and a shallow embayment is present between this cusp and the antero-external cingular cusp F (Text-fig. 5B). This embayment presumably accommodated the posterior surface of M^3 . A narrow internal cingulum runs from cusp E to the base of cusp C (Text-fig. 5C). It supports four minor cusps. The tips of these show some wear. In Text-fig. 5D, a posterior view of the fourth upper molar is shown. It illustrates the relative width of the internal and external cingula.

IV. MOLAR OCCLUSION

Widely differing opinions of the relationship between the two best known families of Triassic mammals, the Morganucodontidae and the Kuehneotheriidae, have been published. Mills (1971: 49), basing his conclusions principally on the structure of the postcanine teeth, stated that the common ancestor of these two families must be placed '... some way below the mammalian level; they may well have evolved from different groups of mammal-like reptiles'. He also stated (*ibid.*: 49) that '... their teeth seem almost as unlike as one could imagine'. On the other hand, Parrington (1967, 1971, 1973), Crompton & Jenkins (1967, 1968) and Hopson &

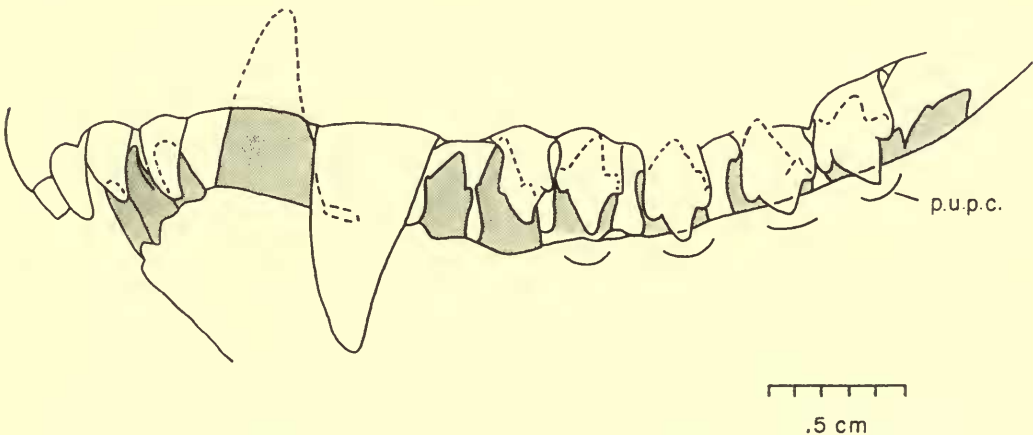


FIG. 8. *Thrinaxodon liorhinus*. Lateral view of the left side of the dentition.

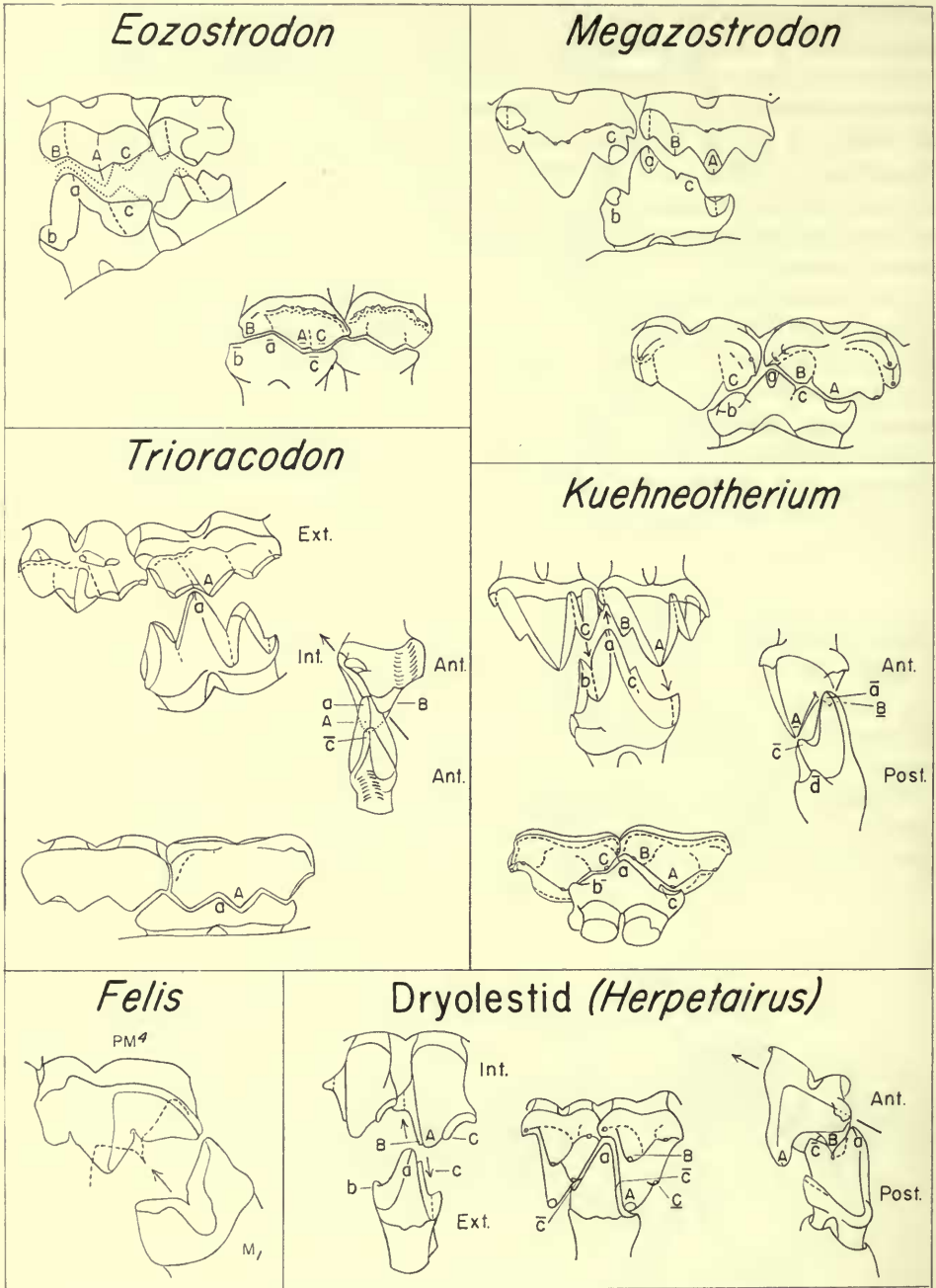


FIG. 9. Diagram illustrating the relative positions of upper and lower molars in a series of Mesozoic mammals and the carnassials of *Felis* sp. *Eozostrodon parvus*, internal view of two upper and external view of two lower molars to illustrate relative positions of occluding molars and an oblique view of the same two molars in occlusion as seen from

Crompton (1969) concluded that the structure and function of the postcanine teeth in the two families are so similar that they were probably closely related. These opposing views are in part based on the differing interpretations of the occlusal pattern in the two groups. Therefore, before discussing the relationships of *Megazostrodon* and *Erythrotherium*, a brief discussion of occlusion in early mammals is pertinent.

In primitive cynodonts such as *Thrinaxodon*, the inner surface of the upper and the external surface of the lower postcanine teeth did not come into contact during occlusion. A narrow space separated the upper and lower postcanine dentitions when the jaws were closed (Crompton & Jenkins 1968, fig. 10). This conclusion is based on a near perfect skull of *Thrinaxodon* completely freed from the matrix by acid. Matching wear facets on the postcanine teeth are absent and therefore during mastication the external surfaces of the lower postcanines were not forced against the internal surfaces of the upper postcanines. The function of these teeth was apparently simply to puncture and tear food. In *Thrinaxodon* the relative positions of upper and lower postcanines varied in different specimens. In the skull illustrated in Text-fig. 8, upper teeth lay directly external to the lower teeth when the jaws were closed. The positions of upper and lower postcanines relative to one another are indicated by shallow pits on the outer surface of the dentary (Text-fig. 8, p.u.p.c.) and on the ventral surface of the maxilla medial to the upper postcanines. Similar pits in the maxilla of *Eozostrodon* have been figured by Parrington (1971). In contrast to the skull illustrated in Text-fig. 8, other specimens of *Thrinaxodon* have upper and lower postcanines alternating with one another.

Thrinaxodon is characterized by alternate tooth replacement and small cusps on the posterior and anterior surfaces of adjoining teeth forming a 'tongue-in-groove' relationship to align the teeth accurately do not exist. Alternate tooth replacement would rule out precise occlusal relationships of the type seen in mammalian molars and the postcanines of some therapsids (Crompton 1972b). In these forms, either the topography of the crowns of the occluding teeth is such that they inherently have accurately matching surfaces or wear resulting from occlusion produces consistent, accurately matching surfaces on specific teeth.

In *Eozostrodon parvus*, Mills (1971) showed that the positions of upper and lower molars relative to one another are the same in all the specimens he studied. Consequently consistent wear facets are produced on molar teeth. As would be expected from this kind of occlusion, the molar teeth are added successively, are not replaced alternately, and small cusps form 'tongue-in-groove' junctions between adjoining molars. It has been shown (Crompton & Jenkins 1968; Parrington 1971; Mills

a ventro-lateral position parallel to the plane of the shearing surfaces. *Megazostrodon rudnerae*, same views of M^1 and M^2 and M_1 . *Trioracodon*, same views plus an anterior view of two molars at the beginning of active occlusion. *Kuehneotherium*, same views. The anterior view of the upper and posterior view of the occluding teeth illustrate the single shearing surface above cusps A and B of the upper molars and below cusps \bar{a} and \bar{c} of the lower. Dryolestid, same views. *Felis* sp., external view of M_1 and internal view of PM^4 to illustrate that the shearing mechanism of the carnassials is the same as that of the principal shearing surfaces in therian molars.

1971; Butler 1972) that in *Eozostrodon* when the jaws were closed, the main cusp \bar{a} of the lower molars lay external to the gap between cusp \underline{B} and cusp \underline{A} of the upper molars (Text-fig. 9, Pl. 3). The main cusp of the uppers (\underline{A}) lay external to the gap between cusp \bar{a} and \bar{c} of the lowers. As a result of the lowers being pressed against the uppers during occlusion, deep wear facets were produced in the areas between the principal and subsidiary cusps to accommodate the principal cusps of the occluding molars. It therefore appears, as has been suggested by Mills (1971), that the gap between cusp \underline{A} and \underline{B} of the uppers and cusp \bar{a} and \bar{c} of the lowers determined the position of upper and lower postcanines relative to one another. However, as has already been pointed out (Crompton & Jenkins 1969; Parrington 1971) when wear commenced, the principal cusp of the lower molar only contacted the inner cingulum of the upper and the principal cusp of the upper only the outer external surface of the lower (see Crompton & Jenkins 1968, figs. 4A₁ and C₁). It is only when wear became more extensive that it extended into the area between the principal cusps and subsidiary cusps. At this stage pronounced wear facets are present on the sides of the principal and subsidiary cusps. Consequently the topography of the crowns of the molars of *Eozostrodon* did not determine the initial contact points between occluding upper and lower molars. This concept is central to the difference of opinion concerning the relationship of the Morganucodontidae and the Kuehneotheriidae. In *Megazostrodon* (Text-fig. 9) which has molars in which the spacing of the three crown cusps, \underline{B} , \underline{A} and \underline{C} and \bar{b} , \bar{a} and \bar{c} , is almost identical to that of *Eozostrodon*, the relative positions of upper and lower postcanines are different. This would not have been the case if the spacing of the cusps determined the relative positions of upper and lower teeth. In *Eozostrodon parvus*, efficient shearing between opposing molar teeth was not possible until wear had produced matching shearing surfaces. In order for these surfaces to be formed consistently in the same positions, the fixing of the relative positions of upper and lower postcanines and the substitution of a mammalian type of tooth replacement for the reptilian alternate tooth replacement was necessary. As shearing planes are only present on worn teeth, there must have been some additional fundamental, but as yet unrecognized advantage to fixing the relative positions of upper and lower molars.

In triconodonts (Text-fig. 9, *Trioracodon*), the relative positions of upper and lower molars are the same as those of *Eozostrodon parvus* (Mills 1971); detailed study of the wear pattern in American Jurassic triconodonts has confirmed Mills' findings. In these forms, the principal cusps \underline{B} , \underline{A} and \underline{C} are more evenly spaced and more similar in height than they are in *Eozostrodon*. The principal cusps of upper and lower molars alternate with one another and the leading edge of the crest joining the individual cusps forms the cutting edge of a series of shearing planes. If the teeth are viewed in the plane of the shearing surfaces (Text-fig. 9, bottom illustration of *Trioracodon*), the cutting edges form a series of V-shaped embrasures (Butler 1972). However, the shearing surfaces of these embrasures differ from the principal shearing surfaces of the molars of therian mammals (see below).

The structure of the principal shearing surfaces of therian mammals is best illustrated in a feline carnassial (Text-fig. 9, *Felis*). Here on the upper PM⁴, an inverted V-shaped ridge connects the paracone to the metastylar region. On the

matching lower M_1 , a V-shaped ridge connects the protoconid and the paraconid. These ridges form the leading or cutting edges of the matching shearing surfaces on the sides of the upper and lower teeth. As these two teeth come into occlusion, the paracone and paraconid meet anteriorly and the metastyle and protoconid meet posteriorly and enclose an ovoid space. As the lower jaw closes, the size of the space progressively diminishes. The advantage of this system is that only two points along opposing cutting edges are closely approximated at any particular moment. These two points move toward the midpoint of the ridge as the jaws close, and the maximum force of the jaws is thus concentrated on a limited area at any given instant in time. The system is therefore ideally suited for slicing through tough food. It has been shown by Dr R. Every (personal communication) and illustrated by Crompton (1971) that the principal shearing surfaces on the anterior and posterior faces of the trigonids and trigons of tribosphenic molars are constructed on the same principle as that operative in the feline carnassial. For purposes of the present discussion, the significant feature of this type of shear is that the matching cusps of upper and lower molars meet point to point at the beginning of shear. This is distinctly different from the triconodontid and eozostrodonid type of shear where the cusps of occluding molars alternate with one another. If the type of occlusion present in *Megazostrodon* were to have been derived from that present in *Eozostrodon*, it would imply a transitional stage in which cusp \underline{A} of the upper (paracone?) would occlude directly with cusp \bar{c} of the lower (metaconid?) and cusp \bar{a} of the lower (protoconid?) with cusp \underline{B} (stylocone?) of the upper. Mills (1971: 45) stated: 'It is very difficult to believe that such an arrangement would be advantageous, or even viable, in a shearing dentition. Although less so, it seems unlikely in a non-shearing reptilian dentition' and 'If cusp stood opposite cusp there would be a greater danger of food jamming the jaw'. What Mills is in fact doubting is the structure of the principal shearing surface of the tribosphenic dentition on the posterior surface of the trigonid and the anterior surface of the upper molar (see Text-fig. 11). In order to avoid the problem of having the sides of the tips of cusps occluding directly with one another, Mills suggested that *Eozostrodon* and *Megazostrodon* were both evolved from a form with molar teeth similar to their premolars. He has suggested a series of steps which imply that cusp \bar{c} of *Eozostrodon* is homologous with cusp \bar{d} of *Megazostrodon* and that cusp 'c' of *Megazostrodon* is a new cusp not present in *Eozostrodon*.

It has been shown that in *Megazostrodon* (Text-figs. 6, 9) the principal cusp of the lower molar lies adjacent to or slightly in front of cusp \underline{B} of the uppers and the main cusp of the uppers lies slightly behind cusp \bar{c} of the lowers. Consequently the arrangement of these cusps relative to one another is similar to that of *Kuehneotherium* and more advanced therians. The principal difference is that in *Megazostrodon* the crests joining these cusps lie approximately parallel to, rather than oblique to, the long axis of the jaw, as is the case in *Kuehneotherium*. The leading edges of the ridges joining these cusps in the unworn molars of *Megazostrodon* do not form the cutting edge of the shearing planes as they do in therian molars. The teeth are bulbous and the wear facets are not extensive in the type specimen. Here, as in *Eozostrodon*, wear commences on the cingular area rather than on the sides of the principal cusps.

Characteristic features of undoubted Triassic mammals were a loss of alternate tooth replacement, differentiation of the postcanine row into premolars and molars, cusps to align adjoining molars, and a consistent relationship between upper and lower molars. In *Eozostrodon* the relationship was such that the principal cusp of the lower lay behind cusp B. As a result, a wide valley was worn into the upper molar between cusps B and A. In *Megazostrodon*, the principal cusp of the lower molar meets the upper molar adjacent to or slightly in front of cusp B. Presumably in specimens of *Megazostrodon* showing extensive wear, the front surface of cusp B would be extensively worn. It appears that *Eozostrodon* and *Megazostrodon* are representatives of an early stage of mammalian dental evolution when the positions of the upper and lower molars relative to one another became established in consistent positions. The differences in the relative positions of the molars of *Eozostrodon* and *Megazostrodon* illustrate that the exact position of upper and lower molars relative to one another was not necessarily identical in closely related genera. It has already been shown that in *Thrinaxodon* the relative positions of the postcanines vary in different individuals of the same genus. Because the principal cusps of both upper and lower molars in *Eozostrodon* and *Megazostrodon* occlude initially with the cingular region of the opposing teeth, the morphology of the crown did not play a major role in determining the relative positions. If, on the contrary, this were the case, the differing occlusal patterns in two forms with very similar teeth would not be expected. From what can be determined, the relative positions of upper and lower molars of *Erythrotherium* are the same as those of *Megazostrodon*; this is despite the fact that the molars of the African *Erythrotherium* are almost identical to those of *Eozostrodon parvus*. This confirms the view that at this early evolutionary stage the occlusal pattern was not determined by the topography of the molar crowns. It is not a question of being obliged to evolve the type of occlusion found in *Megazostrodon* from the type present in *Eozostrodon*, as suggested by Mills (1971), or *vice versa*. It is rather the fixing of the relative positions that is displayed in these two closely related forms. It may not have been very important to these early mammals what the relative positions were, but in terms of evolutionary potential the consequences were far-reaching. From a stage in which the principal cusps of one molar alternated with the subsidiary and principal cusps of the occluding molar, it was possible to evolve the shearing pattern characteristic of the triconodonts; if, on the other hand, the principal cusps lay adjacent to (or slightly in front of, or slightly behind) intermediary cusps of the occluding molar, it was possible to develop the shearing pattern characteristic of therian molars.

Kuehneotherium is important in this context because its molars show an early stage in the evolution of therian shear. Molar occlusion in *Kuehneotherium* has been discussed by Parrington (1967, 1971, 1973), Crompton (1971) and Butler (1972). The pertinent features are shown in Text-fig. 9. The principal cusp \bar{a} of the lower molar (protoconid) occludes directly internal to or slightly in front of cusp B (stylocone) and the principal cusp A of the upper molar (paracone) occludes directly external to or slightly behind cusp \bar{c} (metaconid) of the lower. After the cingulum of the upper molar located above the region between the stylocone and the paracone has been worn away, two matching shearing planes are formed on the front of the

trigon and back of the trigonid. In 1971 (p. 78), I referred to these as shearing plane *I* and have concluded that it is homologous with the shearing plane in the same position on the molars of more advanced therians. Because the tips of the cusps involved come into close contact with one another during occlusion, the trapping ovoid space of therian shearing surfaces was present. However, unlike more advanced therians, this type of shear was not present on the posterior face of the upper molar or the anterior face of the trigonid; this developed in later forms. It is suggested that in forms directly ancestral to *Kuehneotherium* mammalian type tooth replacement was present, and that cusps forming a 'tongue-in-groove' to align adjoining molars were present. As will be discussed in the next section, the cusps involved were slightly different in *Eozostrodon* and in *Kuehneotherium*. It is also suggested that in the forms ancestral to *Kuehneotherium* the principal cusps were in line and that the principal cusps occluded directly with (or slightly behind or in front of) subsidiary cusps. This arrangement helped to trap the food to be sheared.

There is a problem inherent in having the shearing planes aligned parallel to the long axis of the jaw because tough food would tend to separate the shearing blades, much as the blades of a pair of scissors with a loose hinge can be readily forced apart. This problem can be overcome if the shearing blades are oriented oblique to the long axis of the jaw. It is relatively simple to evolve the *Kuehneotherium* arrangement from that of the hypothetical ancestral stage suggested above, simply by migrating the subsidiary cusp \bar{c} (metaconid) slightly medially (internally) and the subsidiary cusp *B* laterally (externally). Given that cusps forming the shearing planes were arranged to trap the food to be sheared, the efficiency of shearing would be improved if the two subsidiary cusps migrated either internally or externally. Parrington (1971) showed that in a series of *Kuehneotherium* teeth the angles between the metaconid and protoconid in the lowers and paracone and stylocone in the uppers vary considerably. In some specimens they are almost in line, whereas in others they form an angle of nearly 90 degrees. It is interesting to note that in *Kuehneotherium* shearing surfaces of the therian type are present only on the posterior face of the trigonid and anterior face of the trigon. Correlated with this is extensive migration of the stylocone and metaconid. In *Kuehneotherium*, cusp \bar{C}^5 of the upper molar and the paraconid do not help to form a therian shearing plane and therefore have not migrated to anything approaching the same extent as the stylocone and the metaconid.

The wear facets of both *Eozostrodon* and *Kuehneotherium* indicate that as the lower jaw closed during mastication, it moved upward and inward during the time when the molar teeth on the active side were in contact. This movement ensures that the chewed food is deposited into the oral cavity rather than remaining between the upper teeth. There is an additional advantage to transverse movements. Kallen & Gans (1972) have determined the contraction sequence of the muscles of mastication in the little brown bat and have concluded that a translatory component during mastication is advantageous as it facilitates tituration and conserves momentum.

⁵ For reasons outlined in an earlier paper (Crompton, 1971) it is doubtful whether cusp \bar{C} is homologous with the therian metacone.

Transverse movements appear to be characteristic of all Triassic mammals and most modern mammals (Mills 1966; Crompton & Hiimäe 1969; Butler 1972). Transverse jaw movement during occlusion implies that if the lower jaw is viewed from directly in front during mastication, a fixed point on the lower jaw such as the tip of a canine will move in a triangular orbit. As the jaw ramus of the active side opens, it moves directly downward and slightly laterally; it continues to move laterally as it starts to close and it moves medially during the final stage of closing. It was probably as a result of the acquisition of rotary jaw movements in forms ancestral to the Triassic mammals that the external surface of lower postcanines was initially brought into contact with the internal surface of the uppers during the final stage of the masticatory orbit. Bringing the postcanines closer into contact improved the ability to break down food. The loss of alternate tooth replacement, fixing of the relative positions of upper and lower molars, and the alignment of adjoining molars seem to have been features which may well have been selected for after the translatory movement of the jaw was established. There would be little point in selecting for these features unless upper and lower molars were brought into close contact with one another. However, if shearing planes are parallel to the long axis of the jaw, a marked transverse movement during active occlusion would tend to separate the cutting edges. One obvious way to overcome this is to orient the principal shearing planes oblique to the jaw axis. This can be achieved simply by the migration of the subsidiary cusps; *Kuehneotherium* represents an early stage in this development. Having the lower jaw move in a triangular orbit around the longitudinal axis of the jaw requires precise control by the jaw musculature; once this has been achieved, the shearing planes of the occluding teeth can be brought into contact accurately. Without it, the fragile cusps and sharp cutting edges of the teeth could easily be damaged. Precise muscular control of the lower jaw during mastication was independently acquired apparently by mammals and gomphodont cynodonts (plus their descendants, the tritylodonts (Crompton 1972b)). In these forms matching shearing planes were present on the postcanine teeth. A triangular orbit was also established for the lower jaw, but the jaw movements were restricted to a plane parallel to the longitudinal axis of the jaw (i.e. if the skull was viewed from the side rather than the front, the lower jaw would have subscribed a triangular orbit with the lower jaw moving forward during the opening and beginning of the closing phase and backward as the postcanine teeth came into contact. Transverse jaw movements were not possible in gomphodont cynodonts and tritylodonts.

In pantotheres (Text-fig. 9, Dryolestid) and mammals with tribosphenic dentitions, shearing planes designed to trap food to be sheared were established both on the anterior face of the trigonid and the posterior face of the upper molars. The characteristic 'reversed triangles' of therian molars appear to have been initiated because principal and subsidiary cusps occluded directly with one another and, for reasons outlined above, this was followed by rotation of the subsidiary cusps. In triconodonts, the cusps of occluding molars alternated with one another. From such an arrangement, transversely aligned shearing planes could not have evolved by rotation of the cusps, and could only have been achieved by developing an exceptionally wide, bulky tooth incised by two long, deep V-shaped grooves. Rotating

cusps and thereby evolving the therian pattern is a simpler and more economical way of achieving obliquely aligned shearing planes.

V. THE RELATIONSHIPS OF *ERYTHROTHERIUM PARRINGTONI*

Mills (1971) pointed out that most features of the molars of *Erythrotherium* can be matched within a large collection of the molars of *Eozostrodon parvus*. He concluded that the differences which I listed in 1964 did not justify placing the southern African form in a separate genus. I agree with his conclusion, but more detailed preparation of the type has subsequently revealed differences which warrant retaining *Erythrotherium* as a separate taxon. Both Mills (1971) and Parrington (1971) stressed that the final upper premolar in *Eozostrodon* is as long as the longest molar and rather higher. This is clearly not the case in *Erythrotherium* where the last upper premolar is smaller than the first molar. There is also no trace of a Kühnecone in the first molar of *Erythrotherium*, but all molars of *Eozostrodon parvus* appear to have a Kühnecone. The relationship between *Erythrotherium* and *Eozostrodon parvus* and *E. oehleri* is, however, extremely close, indicating that the morganucodontids as a group, with many characters held in common, had a wide distribution in late Triassic times, including Europe, China and southern Africa. On the last two continents, early mammals are found together with tritylodontids, and as tritylodontids have been reported from North America (Lewis, Irwin & Wilson 1961) and South America (Bonaparte 1971), it is possible that morganucodontids will eventually be found on these continents as well.

VI. THE RELATIONSHIPS OF *MEGAZOSTRODON RUDNERAE*

In our earlier description (Crompton & Jenkins 1968), *Megazostrodon* and *Eozostrodon* were stated to be closely allied. We followed Parrington (1967) in placing both genera within the Order Triconodonta. In our subsequent paper (Hopson & Crompton 1969), *Megazostrodon*, *Eozostrodon parvus*, *E. oehleri*, *Erythrotherium parringtoni*, and *Sinoconodon rigneyi* were placed in the Family Eozostroodontidae. Hopson (1970) later pointed out that the family name Morganucodontidae had priority. More recently, on the basis of dental occlusion and the relationship between adjacent molars, Mills (1971) placed *Megazostrodon* and *Sinoconodon* in a new family, the Sinoconodontidae. In this section of the paper, *Megazostrodon* will be compared with *Sinoconodon*, *Eozostrodon*, *Docodon* and *Kuehneotherium*.

1. *Sinoconodon rigneyi*

Mills (1971) placed particular emphasis on the similarities between the way in which the adjoining lower molars of *Sinoconodon* and *Megazostrodon* contact one another. In *Megazostrodon*, cusp \bar{d} of a lower molar is in line with cusp \bar{b} of the following molar. In the first and second molars of *Megazostrodon* the tip of cusp \bar{d} has been obliterated through wear, but a sufficient area of the crown in this region

Morganucodontidae

1. Triangular orbit for active side of jaw.
2. Cusps and A contact opposing cingula in consistent positions in different genera.
3. Cusps in line.
4. Mammalian type of tooth replacement.
5. Loss of anterior premolars.
6. Cusp B low.
7. Adjoining molars accurately aligned.
8. Cingulum cusps (external upper and internal lower) well developed.
9. PM₅ highly variable.

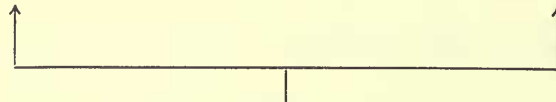
Kuehneotheriidae

1. Triangular orbit for active side of jaw.
2. Cusp a internal to B; A external to c (slight variation).
3. Rotation of cusps to form therian-type shearing surfaces.
4. Mammalian type of tooth replacement.
5. No loss of anterior premolars.
6. Increase in height of cusp B.
7. Adjoining molars accurately aligned.
8. Cingular cusps absent and development of cingulum on outer surface of lower molars.

A

Hypothetical Stage A

1. Triangular orbit for active side of jaw.
2. Cusp a internal to B; cusp A external to c (slight variation).
3. Cusps in line.
4. Mammalian type of tooth replacement.
5. Loss of anterior premolars.
6. Cusp B low.
7. Adjoining molars accurately aligned.
8. Cingular cusps reduced in size.

*Hypothetical Stage B*

(earliest mammal or cynodont group from which mammals arose)

1. Triangular orbit for active side of jaw.
2. Cusps a and A of molars contact opposing cingula, but contact points variable.
3. Cusps in line.
4. Mammalian type of tooth replacement.
5. Loss of anterior premolars.
6. Cusp B low.
7. Adjacent molars in close contact.
8. Cusps on internal cingulum of lowers and external cingulum of uppers prominent. Internal cingulum on uppers moderately developed.

*Galesauridae*

(Early Triassic cynodonts)

1. Jaw movement in vertical plane.
2. No contact between upper and lower postcanines; relative positions variable.
3. Cusps in line.
4. Alternate tooth replacement.
5. Loss of anterior postcanines.
6. Cusp B low.
7. Adjoining molars not accurately aligned.
8. Cusps on internal cingulum of lowers prominent. Cingulum and cingular cusps of uppers poorly developed.

is preserved to determine approximately the position of the tip prior to wear. In lateral view, the tip of cusp \bar{d} lies below the tip of cusp \bar{b} of the following tooth (see Text-fig. 6A). The posterior region of the tooth medial to cusp \bar{d} in *Megazostrodon* as seen in crown view is narrow (the 'talonid'). This fits into a shallow concavity on the anterior surface of the following tooth (see M^1 and M^2 , Text-fig. 6B) this concavity is flanked medially by the enlarged cusp \bar{e} and laterally by cusp \bar{b} . The relationship between cusps \bar{d} and \bar{b} is therefore identical in *Eozostrodon* and *Megazostrodon*. In *Eozostrodon*, however, the posterior surface of the molar is wide and only a very shallow concavity exists between \bar{b} and \bar{e} . Therefore there is a rather wide, flat contact area between adjoining molars (Text-fig. 3). It should be noted that the more intimate relationship between adjoining lower molars of *Megazostrodon* could quite readily be obtained from the condition in *Eozostrodon* simply by enlarging cusp \bar{e} , moving it slightly forward, and narrowing the posterior region of the preceding molar. The junction of two lower molars of *Eozostrodon* is well shown in the stereophotographs in Pl. 3. The arrangement between adjoining teeth in *Sinoconodon* may be similar to that of *Megazostrodon* (unfortunately this area in *Sinoconodon* has not been adequately figured), but as the condition in *Megazostrodon* is so similar to that of *Eozostrodon*, this feature is not a valid reason for placing *Sinoconodon* and *Megazostrodon* in a family which excludes *Eozostrodon*.

Mills (1971) claimed that it is in terms of dental occlusion that the molar teeth of *Megazostrodon* and *Sinoconodon* most closely resemble one another. Unfortunately Mills does not describe the wear facets of *Sinoconodon*. Judging by the loss of all the premolars in the type specimen, it was an old individual and well-defined wear facets would be expected. Mills' conclusions on the relative positions of the upper and lower molars in *Sinoconodon* appear to be based to a large extent upon the spacing of the main cusps. However, as has been shown in the previous section, it is not possible to predict the occlusal relationships between upper and lower molars of Morganucodontids from this feature alone.

Although the relative positions of upper and lower molars of *Megazostrodon* and *Sinoconodon* may prove to be identical, there are some striking differences between these two genera. The external cingulum of the uppers and the internal cingulum of the lowers in *Megazostrodon* are enormously developed. Contrast this with the poor development or even total absence of internal and external cingula on the uppers and lowers of *Sinoconodon*. Even the ubiquitous Kühnecone is absent in *Sinoconodon*. In contrast to *Megazostrodon*, in *Sinoconodon* lower molar cusp \bar{e} is widely separated in height from \bar{b} . In the type jaw of *Sinoconodon* the last molar was not fully erupted, but all the premolars had already been lost. This is not the case in *Megazostrodon* where the molars are all fully erupted and the premolar loss appears to have commenced only on one side of the lower jaw and to have involved only a single premolar.

It has been suggested (Crompton 1964) that the lower jaw of *Sinoconodon* is similar to that of a galesaurid cynodont and unlike that of *Eozostrodon* or *Megazostrodon*.

FIG. 10. Chart illustrating the stages in the evolution of the principal features of the dentitions of the Morganucodontidae and Kuehneotheriidae.

The individual molars of *Sinoconodon* are almost twice as long as those of *Megazostrodon*. *Sinoconodon* is not well preserved and, because of these differences and doubt about the dental occlusion, it is suggested that *Megazostrodon* and *Sinoconodon* should not be placed in a family which excludes *Eozostrodon*. The differences between the molars of *Megazostrodon* and *Sinoconodon* are so striking and the similarity between those of *Eozostrodon* and *Megazostrodon* so obvious that there is perhaps a valid reason for placing *Sinoconodon* in a separate family, but until better material has been described, it is convenient to retain *Sinoconodon* in the Morganuodontidae (= Eozostroodontidae).

2. *Eozostrodon parvus* (= *Morganucondon watsoni*) and *E. oehleri*

There are many close similarities between the dentitions of *Eozostrodon* and *Megazostrodon* (compare Text-figs. 3 and 6). For instance, note the relative sizes and positions of the principal cusps, the positions of cingula, the well-developed Kühnecones and the absence of occlusion between the anterior upper and lower premolars. These similarities, in addition to the structures of the skull and skeleton (to be described in later papers), appear to indicate a close relationship between the two genera. The differences in molar structure of *Megazostrodon* and *Eozostrodon* are in part differences in the relative size of cusps and cingula. For example, in *Megazostrodon* the cingula and cingular cusps, cusp \bar{e} and the Kühnecone are considerably larger than in *Eozostrodon*.

A fairly marked distinction between *Megazostrodon* and *Eozostrodon* is that in the former the last upper premolars are not larger than the first molar; the reverse is true for *Eozostrodon*. The other major difference stressed by Mills (1971) is in the patterns of molar occlusion. This has been discussed in the previous section. In M_2 of *Megazostrodon*, a cingulum is present antero-medial to cusp \bar{e} and a cingulum is present internal to the Kühnecone in M_3 . The cusps of the buccal cingulum of the upper molars of *Megazostrodon* are large and the internal surface is convex; as a result the tooth in crown view is kidney- or bean-shaped. The lingual cingulum of the upper molars is less cuspidate than in *Eozostrodon*. The posterior part (the 'talonid') of the lower molars is relatively longer and narrower in *Megazostrodon* than in *Eozostrodon*. Premolar loss in *Megazostrodon* appears to commence only after the complete eruption of M_4 , and there is no marked decrease in size of the lower molars going in a posterior direction; this is a feature characteristic of many of the lower jaws of *Eozostrodon*.

The extensive loss of anterior postcanines in some individuals of *Eozostrodon* and eruption of a small, apparently non-functional terminal lower molar in *Eozostrodon* are reminiscent of the conditions in cynodonts such as *Thrinaxodon* (Crompton 1963). If premolar loss in *Megazostrodon* was less extensive than in *Eozostrodon*, this could be interpreted as an advanced feature.

The similarities and differences of the molar and occlusal patterns of *Eozostrodon* and *Megazostrodon* suggest that the common ancestor of these genera (Hypothetical Stage B, Text-fig. 10) had molar teeth and a tooth replacement pattern similar to those of *Eozostrodon*. In this common ancestor, during mastication the molars of the active side would have been beginning to contact the cingular areas of opposing

molars. There was probably a significant amount of variation in the relative positions of upper and lower postcanines, but because the upper and lower unworn molars did not have matching shearing planes, the exact position of the initial contact in a young animal was not important. In *Eozostrodon*, the contact point of the cusp \bar{a} of the lower molar was established behind cusp \underline{B} of the upper; in *Megazostrodon*, the contact point was in front of cusp \underline{B} . In addition, in this form the external and internal cingular cusps of the upper and lower molars respectively increase in size, the contact point between adjacent lower molars was modified in a slightly different way from that of *Eozostrodon* and the posterior premolars were not enlarged. Some of the lower postcanines of the Morganucodontidae are very similar to those of *Thrinaxodon*, and if it is accepted that the Galesauridae (= Thrinaxodontidae) included the ancestors of the Morganucodontidae, the main steps that seem to have taken place in evolving the postcanine dentition of the latter from the former are:

(1) Establishing a triangular masticatory orbit for the active side of the lower jaw (see p. 422) so that the postcanine teeth were brought into contact during mastication. Initially it was presumably only the posterior postcanines which came into contact. This is inferred because in the Morganucodontidae the anterior premolars still did not contact one another during mastication.

(2) Developing a mammalian type of tooth replacement in which the milk molars are replaced once by premolars and molars which were not replaced added sequentially from front to back. The steps involved in the transition have been discussed by Osborn and Crompton (1972). *Thrinaxodon* is characterized by loss of several of the anterior postcanine teeth, and this feature is also characteristic of the Morganucodontidae.

(3) Establishing a fixed relationship between the upper and lower molars and developing small cusps to align adjoining molars. This was achieved in slightly different ways in *Eozostrodon* and *Megazostrodon*.

3. *Docodon*

It is generally accepted that lower molars of *Eozostrodon* are similar to those of *Docodon* and that it is possible to derive the latter from the former. However, the upper molars of *Docodon* differ from those of *Eozostrodon* in possessing a well-developed internal cusp which bites into the basin formed between two adjacent lower molars. Crompton and Jenkins (1968) attempted to show how the transition from *Eozostrodon*-type upper molars to *Docodon*-type upper molars could have taken place. Several aspects of the dentition of *Megazostrodon* are reminiscent of *Docodon* (Jenkins 1969). For example, the antero-internal cusp \bar{e} of the lowers of *Megazostrodon* is enlarged, making the anterior region of the crown relatively wider than it is in *Eozostrodon* (see Crompton & Jenkins 1968, fig. 7). A cingulum is present anterior to cusp \bar{e} in *Megazostrodon* and a similar feature is present in *Docodon*. In *Docodon* the Kühnecone is larger than in any of the morganucodontids and of these it is largest in *Megazostrodon*. In M_3 of *Megazostrodon* cusp \bar{c} is considerably reduced in size and in *Docodon* it is absent. It has been suggested (Crompton & Jenkins 1968) that the development of the medial cusp of the upper molars of *Docodon* was in part related to a decrease in size and ultimate disappearance of cusp \bar{c} .

However, the enlarged external cingulum of the upper molars of *Megazostrodon* is not found in *Docodon* where this feature is poorly developed. This evidence suggests that *Docodon* was probably derived from an as-yet-unknown eozostroodontid rather than specifically from *Eozostrodon* or *Megazostrodon*.

4. *Kuehneotherium praecursoris*

Mills (1971) stated that there is a fundamental difference between the molars of *Kuehneotherium* and *Eozostrodon*. In *Kuehneotherium* (Text-fig. 7), the principal cusps form a triangle, obtuse in the anterior molars and more acute in the posterior (Parrington 1967, 1971, 1973); cusps \bar{b} and \bar{c} are high and distinct from the cingulum. In *Eozostrodon*, on the other hand, \bar{b} is low and has been termed a cingular cusp by Mills. In *Kuehneotherium*, the internal cingula of the uppers are narrow and non-cuspidate, whereas they are cuspidate in *Eozostrodon*. There is a weak external cingulum in the lowers of *Kuehneotherium*; in *Eozostrodon* it is at most present in the form of an occasional cusplule (Parrington 1971). The strongly cuspidate internal cingulum of the lowers of *Eozostrodon* is absent in *Kuehneotherium*. In *Kuehneotherium* a small 'talonid' heel supporting cusp \bar{d} is present. It projects between cusps \bar{e} and \bar{f} on the anterior surface of the succeeding molar. In *Eozostrodon*, a distinct 'talonid' heel is absent but the broad posterior region of the molar fits into a shallow embayment between cusps \bar{b} and \bar{e} on the succeeding molar. The other difference between *Eozostrodon* and *Kuehneotherium* is the relative position of the upper and lower molars (discussed on p. 420).

Although the molars of *Megazostrodon* are similar to those of *Eozostrodon*, the former possess some of the features which characterize *Kuehneotherium*. For example, the relative positions of upper and lower molars is the same, the internal cingulum of the uppers of both *Megazostrodon* and *Kuehneotherium* is poorly developed, and the three main cusps of M^1 and M^2 of *Megazostrodon*, rather than being in line, form an obtuse triangle. In these two molars in *Megazostrodon* the external surface of the crown is concave and the internal surface convex; this is also true of *Kuehneotherium* molars. In M_1 and M_2 of *Megazostrodon* a 'talonid' is present and fits into a shallow embayment on the anterior surface of the succeeding tooth. This lies between cusp \bar{e} and cusp \bar{b} in *Megazostrodon*, whereas in *Kuehneotherium* it lies between cusps \bar{e} and \bar{f} . This difference may be related to the more medial position of cusp \bar{b} in *Kuehneotherium*; in this case cusp \bar{f} would have developed to form an outer wall to the embayment. Cusp \bar{b} becomes separate from cusp \bar{a} at a higher level in *Kuehneotherium* than in *Eozostrodon*. In *Kuehneotherium*, cusp \bar{b} is widely separated from cusps \bar{e} and \bar{f} ; in *Megazostrodon*, on the other hand, cusp \bar{e} is large and lies slightly in front of cusp \bar{b} so that cusp \bar{b} appears to be more of a crown cusp than a cingular cusp. Mills draws a sharp distinction between cingular and crown cusps, and on this basis has claimed that cusps \bar{b} of *Kuehneotherium* and of *Eozostrodon* are not homologous. However, it has been shown in *Megazostrodon* that clearly homologous cusps may appear in one molar of a postcanine row as a cingular cusp and in another as a crown cusp. Except for the strong external cingulum, upper M^1 of *Megazostrodon* bears a striking resemblance to Sy_7 of Parrington (1971, fig. 13). The actual advanced feature of *Kuehneotherium* molars is that less of

the tooth has to be worn away to produce the wear facets on the posterior surface of the trigonid and anterior face of the trigon. In addition, this facet is oblique to the longitudinal axis of the jaw.

Mills (1971) stressed the differences in morphology of the molar roots of *Eozostrodon* and *Kuehneotherium*. Although *Megazostrodon* is a mature individual, there are no indications of expansion of the root tips. This problem has been fully discussed by Parrington (1973). In *Kuehneotherium* there is no evidence of the loss of anterior premolars with increasing maturity. In the single specimen of *Megazostrodon*, only one of the premolars appears to have been lost.

Given the range of variation of the molar patterns of the Morganucodontidae, the most significant differences between the known members of this family and the Kuehneotheriidae appear to be: (1) the way in which the adjoining lower molars meet one another and (2) the rotation of some of the subsidiary cusps to form shearing planes oriented obliquely to the longitudinal axis of the jaw.

In Text-fig. 10, the steps in evolving the dentitions of these two families of Triassic mammals from a form of galesaurid such as *Thrinaxodon* are summarized. Two hypothetical intermediate stages have been postulated in the evolution of the dentition of *Kuehneotherium*. In Hypothetical Stage B (ancestral to both the Morganucodontidae and Kuehneotheriidae) the common features of both families are present, including a triangular masticatory orbit, postcanine teeth beginning to contact one another during mastication, mammalian type of tooth replacement and close contact between adjoining molars.

In forms where the postcanine teeth contact one another and where a fixed relationship has been established between upper and lower teeth, the advantage of accurately aligning adjoining molars is that it helps position the teeth accurately as they erupt (Hopson, personal communication). As molar occlusion became more effective in the lines leading to the eozostrodonids and kuehneotheriids, the way in which the molars were aligned developed slightly differently in each. In the line leading to morganucodontids, this was formed by the posterior part of one molar fitting into a shallow embayment between cusp \bar{e} and cusp \bar{b} ; in the latter line by cusp \bar{d} fitting into an embayment between cusp \bar{e} and a new cusp, \bar{f} . The presence of this latter feature, a reduction of the size of the cingular cusps and a fixing of the relative positions of upper and lower molars would have been characteristic features of a Hypothetical Stage A form. The Kuehneotheriidae could have evolved from this stage by rotating the cusps (see discussion on molar occlusion, p. 415), retaining the anterior premolars for a longer portion of the life span, increasing the height of cusp \bar{b} and reducing the cingular cusps further.

If this analysis is correct, it would suggest that both the Kuehneotheriidae and the Morganucodontidae could have been derived from an advanced galesaurid cynodont in which a triangular masticatory orbit had been established. The middle Triassic cynodont *Probainognathus* (Romer 1969, 1970; Crompton 1972a) appears to be closely related to the phylogenetic line between a galesaurid and Hypothetical Stage B. In *Probainognathus*, the dentary forms part of the articulation with the squamosal, the postcanine teeth appear to have contacted one another during mastication, and the tooth replacement pattern is more mammalian than in

Thrinaxodon (J. Osborn, personal communication). *Probainognathus* does not appear to have been on the direct phylogenetic line leading to the Kuehneotheriidae and Morganucodontidae because the cingular cusps, although present, are less well developed than in *Thrinaxodon*.

5. Amphilestinae

Mills (1971) pointed out the strong similarity between the teeth of the Amphilestinae and *Kuehneotherium*; he suggested that these forms be removed from the Triconodontidae. Mills noted that in the Amphilestinae the principal upper molar cusp \bar{A} sheared either against cusp \bar{d} or cusp \bar{b} of the succeeding lower molar. Judging from stereophotographs of a left ramus of *Amphilestes broderipii* in the University Museum at Oxford, the principal cusp of the upper molar occluded between cusps \bar{f} and \bar{b} and in this respect they resemble the late Jurassic symmetrodont *Tinodon* (Crompton & Jenkins 1968) more than *Kuehneotherium*. If a close relationship between the amphilestines, *Kuehneotherium*, and the late symmetrodonts is confirmed, it will support the view that the triangular arrangement of the principal cusps in therians was derived from a form in which these cusps were more nearly in a straight line. It may, therefore, have been possible to derive the Amphilestinae from Hypothetical Stage A (Text-fig. 10). It is interesting to note that in this family both cusps \bar{e} and \bar{f} are present and that the way in which lower molars contact one another is probably the same as in *Kuehneotherium*.

6. Haramiyidae

The isolated teeth of the Haramiyidae (Parrington 1946) remain an enigma, but on the basis of the morphology of the posterior premolars and anterior molars of the Guimarota multituberculate, Hahn (1969) suggested that the haramiyid teeth may have been present in an early mammal which was related to, or ancestral to, the multituberculates. If this comparison is valid, it may be possible to determine the position of some of the haramiyid molars. For example, the teeth assigned to *Microcleptes moorei* (Simpson 1928) may be upper postcanines. In this case, the row of three cusps would be homologous to the principal cusps of the morganucodontids (cusps \bar{B} , \bar{A} and \bar{C}), and the outer cusp row consisting of a high anterior cusp followed by a series of smaller cusps would be homologous to the cingular cusps of morganucodontids. *Megazostrodon* is characterized by a well-developed external cingulum on the upper molars; on M^2 , M^3 and M^4 the anterior cingular cusp is the largest of the cingular cusps. This is extremely slender evidence upon which to base a haramiyid-morganucodontid relationship, and at the most suggests that the haramiyid molars could have been derived from a form ancestral to the Morganucodontidae by enlargement and modification of the cingular cusps.

The wear patterns of haramiyid teeth have not been studied in detail, but some of the heavily worn specimens suggest a triangular masticatory orbit having a power stroke with a transverse component. If this is true, it would mean that the anterior to posterior (or posterior to anterior) power stroke of the multituberculates must have been a secondary specialization in this group, much the same as it subsequently was in some rodents. The basic pattern of mammalian jaw musculature having

been established, it would have been relatively simple for rodents to shift the direction of the power stroke because the lower jaw is held suspended in a sling of musculature (Hiimäe 1971).

VII. CONCLUSIONS

A detailed study of the dentitions of *Erythrotherium parringtoni* and *Megazostrodon rudnerae* has shown that these forms are closely related to *Eozostrodon* (= *Morganucodon*) *parvus* and *E. oehleri* and that they should all be included in the Family Morganucodontidae (= Eozostrodontidae). *Sinoconodon rigneyi* is poorly known and it is suggested that it should also perhaps be included in this family. It is concluded that there is no convincing reason supporting Mills' (1971) suggestion that *Sinoconodon* and *Megazostrodon* be placed in a separate family, the *Sinoconodontidae*, in which *Eozostrodon* and *Erythrotherium* are not included. If this family is to be retained, it should include only *Sinoconodon* and certainly not *Megazostrodon*.

The principal differences between the dentitions of the different genera included in the Morganucodontidae are the degree of development of the cingular cusps of the molars, the relative sizes of the last premolars, and the positions of upper and lower molars relative to one another.

A study of molar occlusion in the triconodonts has confirmed the generally accepted view that this group could have been derived from morganucodontids in which the relative positions of upper and lower molars were similar to that in *Eozostrodon*, rather than that in *Megazostrodon* and *Erythrotherium*. It is tentatively suggested that the molars of the haramiyids could possibly have been derived from a form immediately ancestral to the Morganucodontidae.

It has been concluded that the dentitions of the Morganucodontidae and of the Kuehneotheriidae are sufficiently alike to suggest a fairly close relationship. The principal differences are the way in which adjoining lower molars contact one another, a rotation of the subsidiary cusps in the latter family, and the presence on each molar of at least one major therian-type shearing surface which is aligned oblique to the long axis of the jaw in the Kuehneotheriidae. The dentitions of both families could have been derived from an advanced galesaurid (= thrinaxodontid). The way in which the lower molars of *Amphilestes* meet one another confirms the view that these forms are more closely related to *Kuehneotherium* than to the Morganucodontidae. *Amphilestes* appears to have arisen from the same group that gave rise to kuehneotheriids. The cusps of the amphilestines are in line, and this supports the view that the triangular arrangement of the cusps of *Kuehneotherium* arose by rotation of the subsidiary cusps rather than by the development of new cusps on the flanks of the principal cusps.

On the basis of wear surfaces on the molars, it is confirmed that in all the Triassic mammals, only one side of the jaw was actively involved in mastication at any one time and that during the final stages of jaw closure the jaw moved not only vertically but slightly medially as well. Consequently, if the active lower jaw were viewed from directly in front, during mastication the long axis of the jaw (and naturally

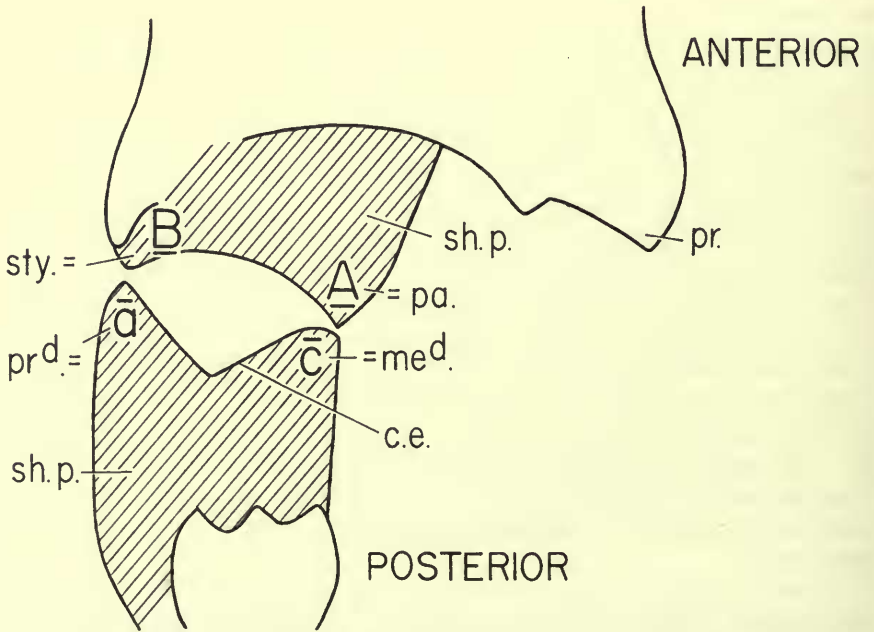
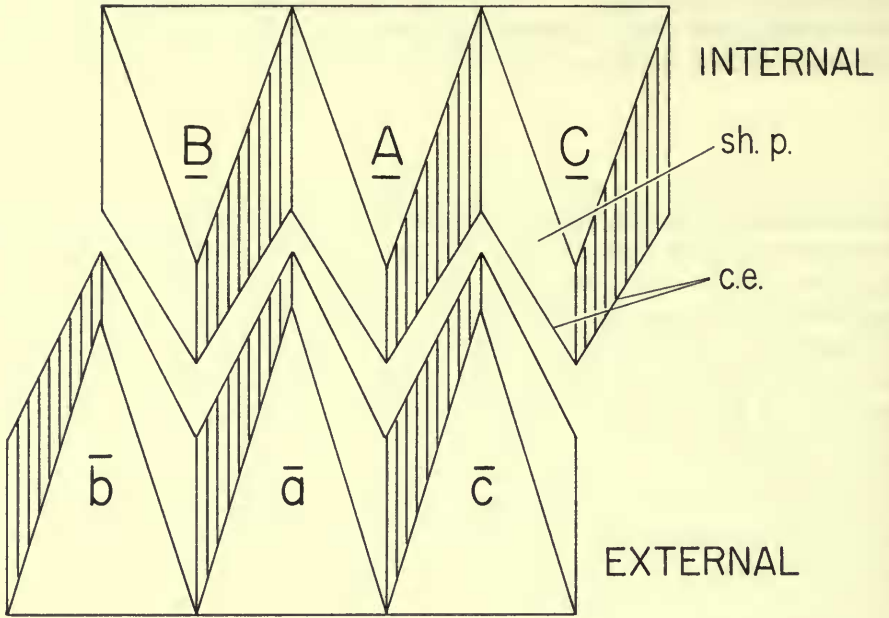


FIG. 11. Comparison of the principal shearing surfaces in the molars of triconodonts and therian mammals. See the text for explanation.

also the individual teeth) would move in a triangular orbit. As the jaw opened and started to close, it moved laterally and as the teeth approached one another until the jaw was fully closed, it moved vertically and medially. It appears that in the Galesauridae (= Thrinaxodontidae), which appear to have been ancestral to the Triassic mammals, the opening and closing jaw movements were restricted to the vertical plane; the sides of the postcanine teeth were not brought into close contact during the final stages of mastication and food was possibly broken up by both sides of the jaw simultaneously. (This latter feature is also characteristic of gomphodont cynodonts.) Therefore, matching shearing surfaces are not found on the postcanines of the Galesauridae. With the introduction of a triangular orbit for the lower jaw, the lower postcanines were brought into closer contact during the chewing cycle. This must have improved the ability of these teeth to break down food. Their efficiency would have been further increased if they developed accurately matching shearing planes on upper and lower postcanines. This required two important changes: (1) fixing the positions of upper and lower postcanines relative to one another and (2) modification of the alternate tooth replacement pattern to one in which the molars are added in both upper and lower jaws sequentially from front to back. In therians, shearing surfaces on a single molar are matched by those on two molars of the opposite jaw. Alternate replacement would disrupt these shearing planes. Once these changes had been incorporated into the dentitions, it was possible to develop consistent, accurately matching shearing surfaces on individual postcanine teeth. The position and morphology of these shearing surfaces in later mammals were initially determined by the relative positions of upper and lower postcanines in the earliest mammals. In the Jurassic triconodonts, the cusps of the upper and lower molars alternated with one another resulting in cusps of one molar shearing down V-shaped grooves between the cusps on the occluding molar and *vice versa* (see Text-fig. 11A). This appears to have developed from the pattern in Triassic mammals such as *Eozostrodon* where the principal cusp of the lower molar initially contacted the cingulum of the upper postcanine external to the gap between its principal cusp A and its anterior subsidiary cusp B.

In therian mammals, the principal shearing surfaces (Text-fig. 11B) are not present on the sides of the V-shaped grooves between the main cusps. Rather, a single shearing surface lies above or below two cusps and the ridge joining the tips of the two cusps forms the leading or cutting edge of a single shearing surface. Consequently, the sides of the tips of the cusps involved meet one another, rather than alternating. In the therian type of shearing, the food to be sheared is trapped in the ovoid space between the four cusps involved. This type of shear appears to have evolved from Triassic mammals in which the principal cusp of the upper molar initially contacted the cingulum of the lower molar directly external to or slightly behind the posterior subsidiary cusp of the lower, cusp \bar{c} , and the principal cusp of the lower molar contacted the cingular area of the upper directly internal to or slightly in front of the anterior subsidiary cusp B of the upper molar. The rotation of the cusps in therians appears to be an adaptation to keeping the principal shearing surfaces in contact as the transverse component of the masticatory orbit increased in magnitude.

In *Amphilestes*, the relative position of upper and lower molars is slightly different from that of the kuehneotheriids. This confirms the view that this was a highly variable feature in early mammals, and that in the different phyletic lines different positions were selected for.

As is well known, the cynodonts are all characterized by a progressive increase in the size of the dentary and relative increase in the mass of jaw musculature. As a result, in advanced cynodonts the jaw joint, despite the surangular-squamosal contact, tended to be relatively less substantial than in the earlier therapsids. In order to reduce the forces acting through the jaw joint, the jaw muscles evolved so as to increase the power of the bite across the postcanine teeth without placing undue strain on the jaw articulation. An important advantage of this type of arrangement of jaw musculature was increased control and mobility of the lower jaw, permitting not only vertical opening and closing movements, coupled with varying degrees of antero-posterior movement, but also permitting transverse movement of the jaw to take place. A result of this was that the longitudinal axis of the lower jaw could follow a triangular orbit during mastication. Consequently, the sides of the upper and lower postcanines on one side could be brought into closer contact than was possible in the earlier carnivorous cynodonts. In addition, the jaw movements could be sufficiently controlled so that occluding teeth were not damaged by malocclusion. The other mammalian features of the masticatory apparatus, the tooth replacement pattern and consistent and accurately matching shearing planes on occluding molars could only develop once the increased mobility, but more important, the precise control of the lower jaw had evolved. This control appears to have been a spin-off from offloading of the jaw joint. In cynodonts and mammals it was probably only when the bite was across the postcanine teeth that the vertical forces acting through the jaw joint could be reduced because of the arrangement of the muscles. If the front of the jaw was used, the jaw joint would have been load bearing (Hiemäe 1971). It may be possible to correlate the rapid evolution in size and complexity of the postcanine teeth in these groups with this feature. The more primitive therapsids, the therocephalians and gorgonopsids, are characterized by powerful incisors and canines and rather weak postcanines. The reverse is true of the Triassic mammals and advanced cynodonts.

The gomphodont cynodonts and tritylodontids which also substantially reduced the size of the jaw articulation had to meet the problem of reducing the forces across the jaw joint at the same time as they increased the power of bite across the postcanines. The jaw muscle arrangement which evolved in these groups also permitted a greater mobility and control of the lower jaw. Matching shearing planes developed on upper and lower postcanine teeth and the reptilian tooth replacement pattern was modified to one in which teeth which had accurately matching shearing surfaces were added sequentially at the posterior end of the row. In addition, the postcanine row was not disrupted by alternate tooth replacement. However, in these forms jaw movements were vertical or parallel to the postcanine tooth rows; transverse jaw movements were not possible. The only therapsid group which substantially reduced the size of the reptilian jaw joint and which also developed a squamosodentary articulation were the ictiosaurs. These retained alternate tooth replacement

of the postcanines and transverse jaw movements were apparently not possible.

The transverse jaw movements, together with the limiting of tooth replacement to deciduous and permanent teeth, the division of the postcanine row into premolars and molars and the fixing of the relative positions of upper and lower molars are characteristic features of all the known Triassic mammals. These features clearly separate Triassic mammals from all known therapsids. It is concluded that this mosaic of features arose in an advanced galesaurid cynodont that lived during middle Triassic time. As far as can be determined at the present time, it is only in the advanced cynodonts that the reptilian jaw musculature underwent the changes which are essential for the evolution of a mammalian type of masticatory apparatus. For this reason it is doubtful whether mammals could be derived from any group other than the cynodonts.

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